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VISUAL NOISE: ITS EFFECT ON PATTERN DISCRIMINATION IN
PIGEONS BEFORE AND AFTER LESIONS OF THE VISUAL SYSTEM

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VISUAL NOISE:
ITS EFFECT ON PATTERN DISCRIMINATION IN PIGEONS
BEFORE AND AFTER LESIONS OF THE VISUAL SYSTEM

by

BEVERLY V. WEST

A dissertation submitted to
the Graduate Faculty in Psychology in
partial fulfillment of the requirements for the degree
of Doctor of Philosophy, The City University of New York

1981

This manuscript has been read and accepted for the Graduate Faculty in Psychology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

5/26/81
date

William S. Butterley
Chairman of Examining Committee

August 25 1981
date

Harold S. Saltzman
Executive Officer

W. J. ...
...
H. P. Zeigler
...
Supervisory Committee

The City University of New York

Abstract

VISUAL NOISE: ITS EFFECT ON PATTERN DISCRIMINATION IN PIGEONS BEFORE AND AFTER LESIONS OF THE VISUAL SYSTEM

by

Beverly V. West

Advisor: Professor William Hodos

Recent anatomical, physiological and behavioral studies of the avian visual system have indicated that like the mammalian colliculofugal visual pathway, the avian tectofugal visual pathway is important in visual function. In both birds and mammals, a number of studies have attempted to analyze the nature of the deficit; i.e., to determine whether a sensory defect or a lack of attention is responsible for the impairments of visual performance following interruption of the tectofugal pathway. A number of these experiments have reported deficits on embedded-figures tests. However, a weakness of these tests has been the paucity of quantitative data on the limits of performance of subjects with tectofugal pathway lesions. The present experiment was an attempt to use quantitative methodology based on psychophysics and information theory in order to gain further insight into the nature of the deficit. The technique used required the subjects to perform a simple visual discrimination in the presence of progressively increasing levels of visual noise. In other words, the subjects

were required to perform at the limits of their ability to extract information from a noisy information channel.

Fourteen pigeons (Columba livia) were trained to discriminate two planometric patterns. Once pattern discrimination was achieved, various percentages of static visual noise were introduced in progressive increments during discrimination testing. Using a variation of the method of constant stimuli, a psychometric function of the degrading effects of added noise on the discrimination was determined. An index of the interfering effects of this noise was derived. This index (Noise Interference Index) reflected the greatest percentage of background noise which the pigeon could tolerate while maintaining a discrimination performance of no less than 75% correct. Discrimination testing was continued until five successive sessions occurred during which the noise interference index was stable.

After satisfying the stability criterion, each pigeon was anesthetized and subjected to bilateral, electrolytic lesions which were stereotaxically aimed at the ectostriatum (the telencephalic target of the tectofugal pathway), visual wulst (telencephalic target of the avian equivalent of the geniculostriate pathway) or control areas.

After postoperative recovery, testing was resumed using the same preoperative procedures.

The results revealed that pigeons with ectostriatum (tectofugal) lesions showed significantly less tolerance to visual noise than did pigeons with visual wulst (geniculostriate) lesions or control lesions. The results indicate that the deficits observed after lesions of the tectofugal pathway may be the result of an inability to suppress the irrelevant aspects of the visual environment. The results are discussed in the context of information theory, attention theory, signal detection and response inhibition. The implications of these findings for research on the mammalian visual system are also discussed.

PREFACE

"Each actual psychophysical process depends on a definite complex of conditions, including:
(a) the total configuration of the stimulus upon the retina in the particular case,
(b) the relatively constant histological and material properties of the optical-somatic system,
(c) the relatively variable conditioning factors attributed primarily to the remainder of the nervous system and secondarily to the vascular system."

W. Köhler, 1920 [p. 262]

No current theoretical statement could more aptly introduce or describe the nature of the dissertation that follows. The Gestalt principles of pattern organization and figure-ground relationships summarize many of the features that the visual system allegedly extracts from pattern stimuli and transmits in simple code to higher levels for further processing. While the traditional Gestaltists' brain model did not afford an adequate explanation of how this psychophysical phenomena could be accomplished, the Gestalt theorists' claim that stimulus configuration is a main determinant of perceptual organization still provokes experimental interest. The work that follows integrates this interest with contemporary theories of information processing in an attempt to provide some insight into the relationship of brain physiology and the perception of stimulus configurations.

This dissertation was skillfully directed by Dr. William Hodos. I am greatly indebted to him and to Drs. William S. Battersby, Pedro Pasik and Jack Orbach for their indispensable guidance.

The author is particularly grateful to her family for reasons too numerous to list and special appreciation is extended to Alexandria Terzian for her artistic and technical assistance in the preparation of the manuscript.

Beverly V. West

TABLE OF CONTENTS

	Page
INTRODUCTION.....	1
EXPERIMENT I. A measurement of the normal capacity of the avian visual system to filter out noise in order to discriminate familiar patterns.....	24
METHOD.....	25
RESULTS.....	39
DISCUSSION.....	47
EXPERIMENT II. A measurement of the effects of ecto- striatal and visual wulst lesions on the capacity of the avian visual system to filter out noise in order to discriminate familiar patterns.....	54
METHOD.....	55
RESULTS.....	59
DISCUSSION.....	117
GENERAL DISCUSSION.....	124
REFERENCES.....	130

LIST OF TABLES

Table	Page
1. Mean Number of Correct Responses Given At Each Noise Level for Each Session.....	40
2. Percentages of the Telencephalon and Components That Were Destroyed.....	60
3. Preoperative and Postoperative Number of Training Trials Required to Reach Criterion.....	93
4. Equations for Preoperative and Postoperative Curves of Best Fit for Noise Interference Functions.....	101
5. Preoperative and Postoperative Comparison of Noise Interference Index Values.....	102

LIST OF FIGURES

Figure	Page
1. Two visual pathways in the pigeon.....	3
2. Some types of embedded figures tests.....	16
3. A visual noise test.....	21
4. Flow chart of training and testing procedures.....	31
5. The noise resistance limit.....	34
6. The noise interference index function.....	37
7. Straight line fit to percent of correct responses obtained at each noise level.....	42
8. Preoperative curves of best fit for noise inter- ference index function for each pigeon.....	46
9. Transverse plane reconstructions of lesions of ectostriatum.....	63
10. Enlarged figure key for transverse brain recon- structions.....	64
11. A microphotograph of an extensive lesion of ecto- striatum.....	66
12. Transverse plane reconstructions of retrograde degeneration in nucleus rotundus following damage to ectostriatum.....	69
13. Parasagittal plane reconstructions of lesions in the visual wulst.....	72
14. Enlarged figure key for parasagittal brain recon- structions.....	73
15. A microphotograph of a moderate lesion of the visual wulst proper.....	77
16. Parasagittal plane reconstructions of control lesions through the caudal neostriatum.....	81
17. A microphotograph of a moderate lesion of caudal neostriatum.....	83

18.	Parasagittal plane reconstructions of lesions through the ventral hyperstriatum that deafferented the visual wulst.....	85
19.	Parasagittal plane reconstructions of lesions through the visual wulst, ventral hyperstriatum and ectostriatum.....	87
20.	A microphotograph illustrating one type of mixed lesion.....	89
21.	Parasagittal plane reconstructions of the extent of retrograde degeneration in nucleus rotundus following damage to ectostriatum, ventral hyperstriatum and visual wulst.....	91
22.	Comparison of the postoperative noise interference index function with the preoperative period of stable performance for pigeons with lesions of ectostriatum...	99
23.	Comparison of the postoperative noise interference index function with the preoperative period of stable performance for pigeons with lesions of visual wulst...	107
24.	Comparison of the postoperative noise interference index function with the preoperative period of stable performance for pigeons with mixed lesions.....	110
25.	Comparison of the postoperative noise interference index function with the preoperative period of stable performance for pigeons in the control group.....	112
26.	A summary of initial and final differences in the noise interference index after telencephalic lesions...	115

INTRODUCTION

Recent examinations of the anatomy, physiology and behavior of avian visual systems have revealed that many vital visual functions depend upon the integrity of two visual pathways ascending to the telencephalon, namely, the tectofugal and thalamofugal visual pathways.* When either of these pathways is disrupted, visual discrimination is impaired. What is the nature of this impairment? Are the behavioral visual losses observed after visual system injury the result of the loss of a specific analyzer function that resides in the injured cells? This question characterizes the general topic of this dissertation. The specific topic of this study is the nature of the defects following injury to the telencephalic components of these pathways in pigeons. These are the ectostriatum (tectofugal component) and the visual wulst (thalamofugal component).

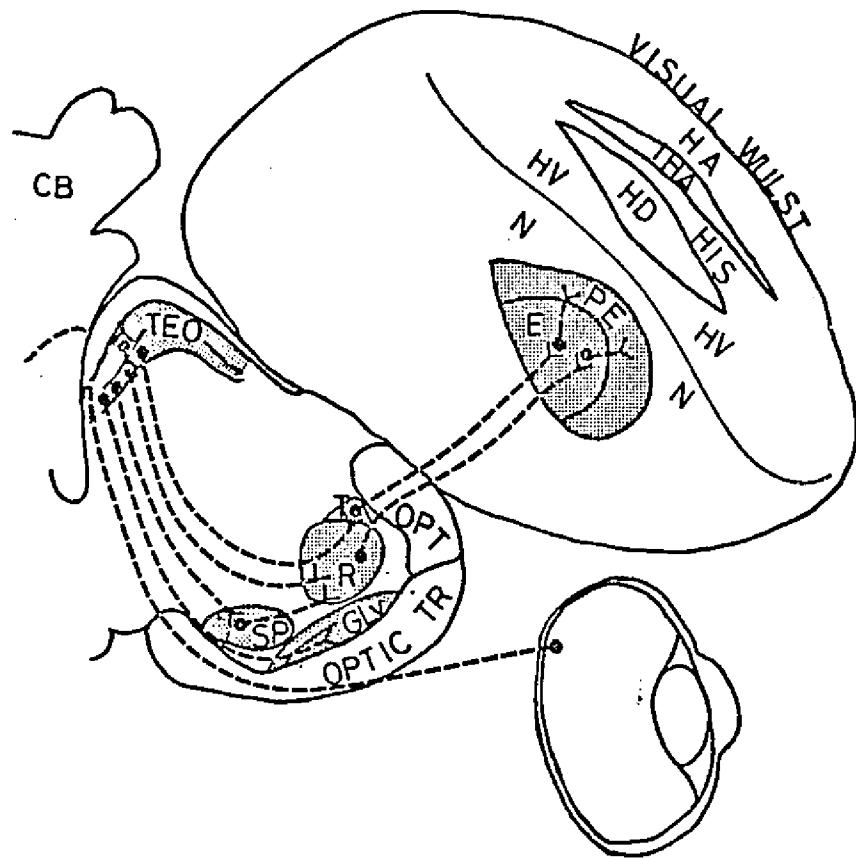
*The terms tectofugal pathway and thalamofugal pathway are misnomers since both pathways have a retinal origin and both have thalamic components. These terms were chosen (Karten, 1969; Karten & Hodos, 1970; Nauta & Karten, 1970; Karten, Hodos, Nauta & Revzin, 1973) to underscore the main fiber sources of these pathways, i.e., the extensive afferentation of nucleus rotundus thalami by the optic tectum in the tectofugal pathway and the extensive afferentation of the telencephalic nuclei hyperstriatum dorsale and intercalatus hyperstriati accessorii by the nucleus opticus principalis thalami in the thalamofugal pathway.

Pigeons are the subjects of choice because the avian system is highly specialized for precision in visual processing (see Hodos, 1976; Donovan, 1978, for review). In comparison to other vertebrate classes, a greater proportion of the central nervous system of birds is devoted to the processing of visual information and the maintenance of visual-motor coordination.

Anatomy and discriminative capacities of tectofugal and thalamofugal pathways

In birds a complete decussation of retinal fibers occurs at the optic chiasm (Perlia, 1889). Upon leaving the chiasm, (Fig. 1) optic fibers terminate in the optic tectum (comparable to the retino-recipient layers of the mammalian superior colliculi), the principal optic nucleus of the thalamus which is comparable to the pars dorsalis of the mammalian lateral geniculate, the pars ventralis of the lateral geniculate nucleus, the pretectal nuclei, the ectomammillary nucleus (medial accessory optic nucleus), the suprachiasmatic hypothalamic nucleus, and the lentiform mesencephalic nucleus (lateral accessory optic nucleus), (Cajal, 1899; Cowan, Adamson & Powell, 1961; Karten & Nauta, 1968; Meier & Cuenod, 1973;

TECTOFUGAL PATHWAY



THALAMOFUGAL PATHWAY

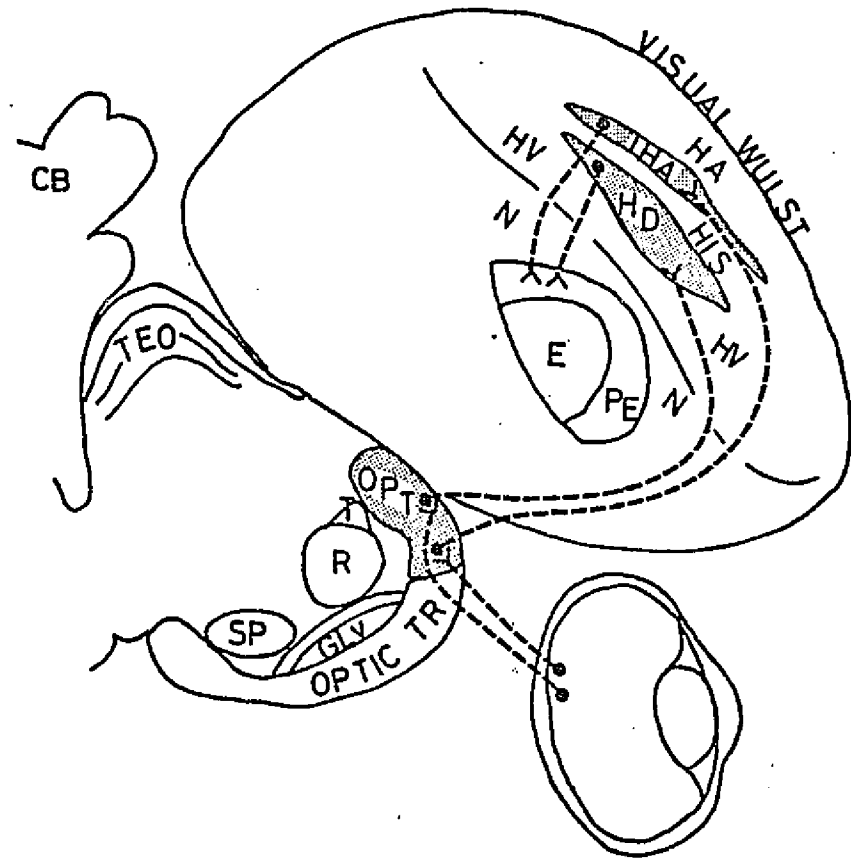


Fig. 1. A parasagittal view of two pathways in the avian visual system.

Abbreviations

CB - cerebellum
E - ectostriatum
GLV - nucleus geniculate lateralis, pars ventralis
HA - hyperstriatum accessorium
HD - hyperstriatum dorsale
HIS - hyperstriatum intercalatus suprema
IHA - nucleus intercalatus hyperstriati accessorii
OPT - nucleus opticus principalis thalami
PE - peri-ectostriatal area
R - nucleus rotundus
SP - nucleus subpretectalis
T - nucleus triangularis
TEO - tectum opticum

Reperant & Angaut, 1977). Because most of the retinal fibers project to the tectum, much of the research on avian visual anatomy has focused on tectofugal pathways. Both anatomical and electrophysiological studies have traced the retinotectal pathway to telencephalic levels (Karten & Revzin, 1966; Karten & Hodos, 1970).

The avian tectofugal tract has been implicated in visual function. Massive lesions of the optic tectum lead to irreversible deficits in difficult pattern discriminations (Hodos & Karten, 1974; Jarvis, 1974). The performance of intensity and simple pattern discrimination is entirely disrupted (Hodos & Karten, 1974). Nucleus rotundus, the thalamic component, is the major thalamic recipient of ascending fibers from the optic tectum (Karten & Revzin, 1966; Revzin & Karten, 1966/1968). Severe bilateral injury to this nucleus also results in impaired performance of brightness and pattern discriminations (Hodos & Karten, 1966; Hodos & Fletcher, 1974; Hodos & Bonbright, 1974). Only after extensive postoperative retraining is there a gradual return to preoperative performance levels.

Some controversy has existed in the literature as to the telencephalic destination of rotundal efferents. Cowan, Adamson and Powell (1961) using retrograde degener-

ation techniques contended that fibers of nucleus rotundus terminate in paleostriatum augmentatum. However, Revzin and Karten (1966/1967) determined electrophysiologically that nucleus rotundus projects mainly to the core of the ectostriatum via the thalamofugal tract and attributed the findings of Cowan and associates (1961) to the interruption of fibers of passage emanating from nucleus rotundus and passing through the lateral portion of paleostriatum augmentatum en route to ectostriatum. Karten and Hodos (1970) using both anterograde and retrograde methods found support for this interpretation. Benowitz and Karten (1976) went a step further in demonstrating a topographical projection of fibers from nucleus rotundus to ectostriatum. Hodos and Karten (1970) reported that bilateral electrolytic lesions of ectostriatum resulted in impaired performance of visual intensity and pattern discriminations. Moreover, a positive correlation was found between the extent of the lesions and the amount of postoperative retraining required for recovery of criterion performance.

A second ascending visual pathway in birds is the thalamofugal tract. This pathway passes from the retina to the principle optic nucleus of the thalamus (OPT), a complex of four nuclear masses, viz., the dorsal and ventral portions of nucleus dorsolateralis anterior, pars lateralis (DLLd and DLLv); nucleus lateralis anterior (LA); and

nucleus dorsolateralis anterior, pars magnocellularis (DLAmc). The OPT in turn sends efferents via the lateral forebrain bundle to a hyperstriatal portion of the telencephalon known as the visual wulst (Cowan, et al., 1961; Powell & Cowan, 1961; Hirshberger, 1967; Karten & Nauta, 1968; Hunt & Webster, 1972; Karten, et al., 1973; Meier, et al., 1974; Miceli, et al., 1975). However, according to Hunt and Webster (1972) and Meier and associates (1974), only the dorsolateral retinal input from DLLd and DLLv project to the visual wulst.

The visual wulst consists of two granule cell layers (the dorsal hyperstriatum (HD), the intercalated nucleus of the accessory hyperstriatum (IHA) as well as two agranular cell layers (the accessory hyperstriatum (HA), the intercalated nucleus of the supreme hyperstriatum (HIS)). Only the "granular wulst" (IHA and HD) receive the fibers from OPT. Moreover, the receptive fields of IHA are described as small, and capable of registering fine detail (Revzin, 1969; O'Flaherty and Invernizzi, 1972). Moreover, Revzin (1969) reported the presence of horizontal detector cells as well as columnar and retinopic organization of UHA cells.

As to the visual behavior that may be mediated by the thalamofugal network, Hodos and Bonbright (1974) observed small permanent increases in intensity difference thresholds in pigeons sustaining damage to the OPT complex. However, no significant or permanent deficits in near field visual acuity

have been observed in pigeons sustaining OPT lesions (Macko, 1978) or lesions of the granular visual wulst (Hodos, et al., in prep). Tuge and Shima (1959) found that two pigeons with total hyperstriatal lesions could not discriminate between a white and a red light when both were used as conditional stimuli. Zeigler (1963) also reported severe deficits in pattern discrimination after ablation of most of the hyperstriatum. These deficits, however, are most likely due to extensive damage to the ventral portion of the hyperstriatum, since lesions restricted to the granular visual wulst result in little or no impairments in pattern and intensity discrimination. Some evidence to support this contention was reported by Macphail (1969; 1971) who failed to observe any detrimental effects of small lesions within the granular visual wulst on simultaneous brightness discrimination; similarly, Hodos, Karten and Bonbright (1973) observed no impairment in the retention of simultaneous discriminations of either brightness or pattern in pigeons sustaining granular visual wulst injury. Thus, the evidence would seem to warrant the conclusion that tectofugal injury induces severe visual deficits while thalamofugal damage does not.

According to Hodos and Bonbright (1974), thalamofugal damage does induce visual defects. The authors explain that impairments in visual discrimination were not evident in previous examinations of pigeons sustaining thalamofugal damage because coarse discrimination tests were used to assess

visual capacity. Coarse discrimination tests are defined as those tests which measure visual responses to gross differences in the intensities or patterns of visual stimuli. Hodos and Bonbright expressed the opinion that a disruption of the thalamofugal pathway induces visual deficiencies which are too subtle to be measured by coarse discrimination tests, e.g., horizontal vs. vertical bars. Thus Hodos and Bonbright (1974) used an alternative measure they had previously developed (1972) which employs a psychophysical technique. This method systematically forces a pigeon to discriminate progressively smaller differences in a visual stimulus. The limit of the pigeon's discriminative capacity is thus determined from the resulting psychometric function. When pigeons with thalamofugal damage were tested with this procedure, the birds displayed increases in light intensity thresholds (Hodos & Bonbright, 1974; Pasternak & Hodos, 1977). Some of the deficits were permanent (Hodos & Bonbright, 1974). Thus, the psychophysical method proved to be more effective in measuring visual dysfunction after thalamofugal injury.

Internal and external visual noise as determinants of visual deficits

As to the nature of visual deficits resulting from tectofugal or thalamofugal damage, Hodos and Bonbright (1974) put forth two hypotheses: First, they postulated that

"visual discrimination impairments reflect the pigeon's inability to filter out extraneous or irrelevant aspects of the visual world". This hypothesis is based on a signal detection analysis of increased intensity difference thresholds which were obtained from pigeons sustaining damage to thalamic components of the visual system (Hodos and Bonbright, 1974). The analysis revealed that postoperative increases in intensity difference thresholds resulted from decreases in stimulus detectability and not changes in response bias or motivational states. In accordance with the assumptions of signal detection theory, Hodos and Bonbright (1974) suggested that disruption of either tectofugal or thalamofugal pathways would increase the internal noise in the visual system, thereby adding to the experimentally induced noise to mask the signal even more. Internal noise, according to Green and Swets (1966) is spontaneous neural activity which is added to all incoming noise or signal plus noise. The adverse effect of internal noise on visual perception has been clearly demonstrated in elderly humans where nerve cell degeneration results in high levels of random neural activity (Welford, 1958). More recently, visual masking experiments which employ external visual noise as masks reveal age differences in humans in backward masking (Kline & Szafran, 1975; Walsh, 1976). That is, the older subjects were found to be more susceptible to the masking effect when long delays were imposed between the target and masking stimulus in a monoptic paradigm

(Szafran, 1975). While in a dichoptic model, elderly subjects took a longer period of time to escape effects (Walsh, 1976). Thus, it is quite possible that neural noise, whether naturally or artificially induced at central levels, can interfere with central processing of visual information in pigeons.

The second hypothesis proposed by Hodos and Bonbright was that the telencephalic components of the visual system are involved in the filtering process, that the function of these components is to relate a visual stimulus to an appropriate context by filtering out irrelevant information.

A recent experiment strongly suggests the necessity for visual filtering. Mezrich (1979) asserted that a band-pass filtering mechanism is required for human visibility of patterns embedded in noise. In an experiment using the contrast reversal effect achieved by Rose's (1974) technique of systematic dot deletion, Mezrich proposed that low-pass spatial filtering acts to enhance the visibility of triangles supported by a dotted background. The solid lines bounding the triangles do not actually exist, thus low-pass filter mechanisms enable the perceptual construct of solid lines in the dot patterns by achieving a connection of the dots to form a uniform background. Thus, there may be a necessity for a visual filtering mechanism in birds whose survival strongly depends upon the ability to visually penetrate animal camouflage or the ability to migrate in weather conditions

of poor visibility.

The goal of this study is twofold: (1) to test the filter hypothesis by first assessing the ability of the intact pigeon's visual system to filter out external noise, and (2) to observe the capacity of the pigeon's visual system to filter out external visual noise after destruction of thalamofugal or tectofugal components.

Some concepts put forth in information theory suggest a method for evaluating the capacity of tectofugal and thalamofugal pathways to filter out irrelevant information. One of the major features of information theory (Shannon, 1948) is its stipulation that the output of any communications system is determined by numerous classes of input variables. Thus, the visual system may be conceptualized as a communications system in which the source of information is equated with the visual stimulus; the transmitter or encoder function is assigned to the retina; and the retino-cortical pathways are designated as channels which dispatch the information to visuo-cortical areas of the brain for signal decoding and response.

Under normal conditions, information can be efficiently transferred in the visual system in spite of the inherent noise level of the channel. However, external influences could introduce additional noise which could have a disruptive effect on information processing. For example, noise may

occur in the encoding or decoding process in the form of extraneous stimuli which interfere with the signal of interest. Or, the limited channel capacity of the system may be exceeded by an extreme rate or quantity of visual input which produces stimulus ambiguity. Thus, the telencephalic decoding areas may be likened to a central scanner or filter which may become unable to identify pattern input when noise input is high.

The principle of limited channel capacity, i.e., the upper limit in the amount of information which can be processed and transmitted by a channel provides a model for testing the filter hypothesis. The channel capacity of any system can be established by running tests that exceed the capabilities of that system. One means of exceeding the transmission capabilities of the visual system is to confound a visual stimulus with very high levels of noise, thereby creating stimulus ambiguity which reduces the visual system's capacity to encode, transmit and decode the stimulus information. This method may provide a means to determine how efficiently the avian telencephalic visual areas filter out noise in order to register relevant pattern inputs.

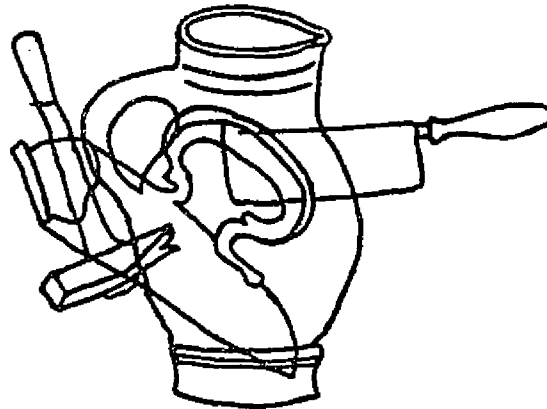
Effects of external noise on visual pattern discrimination

Noise is defined as any stimulus not designated as signal, but which may be confused with it. Thus, in some studies of

visual pattern discrimination an annulus surrounding a pattern to be recognized may be regarded as visual noise. In addition, visual noise may be displayed as a mask of random noise dots presented before or after the presentation of a signal pattern ("dynamic visual noise", e.g., Uttal, 1971). Or, visual noise may be a spatially overlapping mask which is displayed concurrently with the pattern ("static visual noise", e.g., Barlow, 1978).

A considerable number of human and animal pattern discrimination studies have shown that pattern recognition can be reduced by the addition of static visual noise. Moreover, some early reports of the effects of pattern context on visual pattern discrimination suggest types of signal-noise patterns which are effective in creating stimulus ambiguity and also effective in measuring the visual system's response to stimulus ambiguity under normal and damaged conditions. Poppelreuter (1917) developed a perceptual test in which human subjects sustaining injury in visuo-cortical areas were shown mixed figures (i.e., pictures which were scribbled over or superimposed one on another (Fig. 2). The patients were required to pick out a specific figure (signal) from the irrelevant background (noise), or to trace the outlines of the various superimposed figures. Defective performance resulted. A more severe impairment was demonstrated with the more difficult

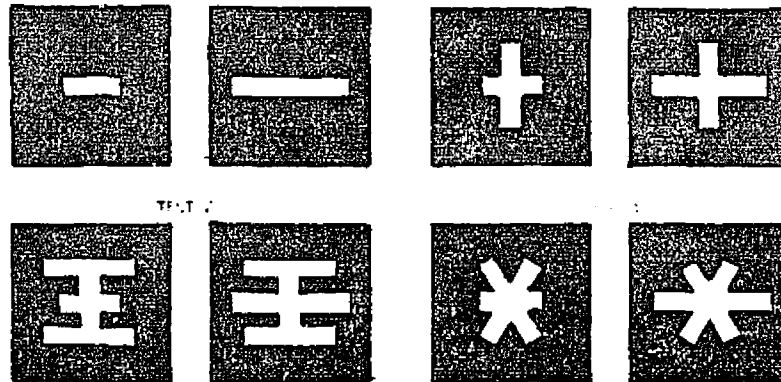
Fig. 2. Some types of mixed-figure and embedded-figure tests that have been used to evaluate visual pattern recognition after injury to visual brain areas in humans (Poppelreuter, 1917; Gottschaldt, 1929), monkeys (Butter, 1969; 1972; Chalupa, et al., 1976), tree shrew (Killackey, et al., 1971) and bushbaby (Atencio, et al., 1975).



Poppelreuter, 1917

Rangplatz d. Schwierigkeit		8 Vpn	
Nr.	Rg. Kl.	a	b
8	m		
9	m		
10	m		
11	s		
12	s		
13	s		
14	s		
15	s		

Gottschaldt, 1929



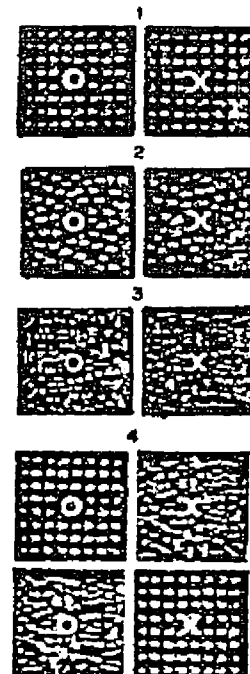
Butter, 1969

DISCRIM. TRAINING

Z E

MASKING TEST

Butter, 1972



Killackey et al., 1971
Chalupa et al., 1976

Atencio et al., 1975

hidden or embedded figures test developed by Gottschaldt (e.g., 1929, Fig. 2). This test is distinguished from the mixed figures test by the sharing of contours or boundaries between the relevant figure (signal) and the background figure (noise).

Variations of these two tests of figure-ground perception are still evident in recent examinations of the effects of pattern content on pattern discrimination. In an experiment by Butter (1969) groups of intact monkeys, monkeys with inferotemporal ablations and monkeys with lateral striate lesions were first trained to discriminate between two visual patterns. Irrelevant features were then added to the discriminanda (Fig. 2) in a series of tests in which the animals were required to relearn the discrimination problem. Monkeys with inferotemporal damage were impaired relative to the normal animals in initial acquisition of the discrimination and in two of the three masked conditions. The monkeys with lateral striate damage, however, were not impaired in acquisition, but were severely impaired in relearning with the addition of irrelevant stimuli. Butter (1972) felt that acuity was the critical factor in the poor test performance of monkeys sustaining striate damage or that the deficit was not specific to lesion locus. In another experiment, Butter (1972) repeated the procedure above but added a third operated group, i.e., monkeys with dorsolateral

frontal lesions. In addition, irrelevant stimuli were added to the discriminanda in such a way that acuity was not a critical factor in test performance, i.e., the discriminanda were not touching the background figures. Again, both inferotemporal and lateral striate lesions led to deficits in mixed-figure discrimination. The performance of the dorsolateral frontal animals was relatively unimpaired. Chalupa and colleagues (1976) found that monkeys with lesions in inferior pulvinar that had difficulty in learning a visual discrimination were further impaired by the addition of irrelevant annuli (Fig. 2). The performance of monkeys with medial and lateral pulvinar lesions as well as normal controls was only temporarily disrupted. Thus, it appears in monkeys that only damage to cerebral areas which have been implicated in visual function will induce deficits in discrimination of visual patterns which are mixed or embedded.

The same is true of other species. In bushbaby, Atencio, Diamond, and Ward (1975) demonstrated that inferotemporally ablated bushbabies require prolonged retraining or meet failure on retention tests of patterns mixed with even or irregular rows of dots (Fig. 2). Postoperative acquisition of the same discrimination was possible in one out of two inferotemporal animals. On the other hand, one out of two bushbabies with bilateral occipital lesions showed difficulty in learning a pattern discrimination postoperatively but when

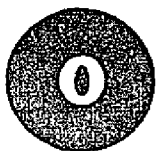
the patterns were mixed with even or irregular placements of dots, relearning the discrimination was possible though prolonged. A parietal control showed no deficit in post-operative acquisition.

In tree shrews, Killackey, Snyder and Diamond (1971) have found that tree shrews without striate cortex are unable to retain or relearn a discrimination between upright and inverted triangles when each is embedded in an annulus (Fig. 2). On the other hand, tree shrews with temporal lobe ablations suffer a retention loss but eventually reattain criterion performance with protracted training.

In summary then, the foregoing evidence points up the efficacy of embedded-figures tests to reveal defects in discriminative ability after damage to either tectofugal or thalamofugal visual components. In each of the foregoing studies, the addition of external static noise reduced pattern recognition. However, the embedded or mixed-figures tests used in those experiments did not measure or quantify the range of discriminative ability before or after visual system injury. As a consequence, the performance deficit on embedded-figures tests appears to be nonspecific in most instances, i.e., equal in magnitude with injury to any cell group in the visual system. The chances that tectofugal and thalamofugal lesions will result in the same degree of impaired discrimination in pigeons is unlikely in view of

the large difference in JND loss already demonstrated with intensity discrimination tests (Hodos & Bonbright, 1974). Thus, the prerequisite for an accurate assessment of the pigeon visual system's capacity to process embedded patterns is a test which will not only measure small impairments in discriminative capacity, but will also quantify the range of discriminative ability that remains after specific visual system injury.

By applying the principle of limited channel capacity, one can ascertain the range of discriminative ability in intact pigeons. This may be accomplished by presenting noise-embedded patterns which continuously vary in the amount of noise. In doing this, one may determine the visual channel capacity or terminal limen of noise that does not prohibit pattern recognition. The dotted stimuli used in the bushbaby study (Atencio, et al., 1975) seem best suited to this type of manipulation. Thus, if a pigeon is repeatedly presented a pattern discrimination test in which the patterns vary continuously in the amount of surrounding noise particles (Fig. 3), one may precisely determine the effect of the presence of varying degrees of external static noise. Thus, the greatest quantity of noise that a pigeon can tolerate while correctly discriminating the stimulus pattern can serve as an index of that pigeon's efficiency to filter out visual noise to register pattern information.



0



6.25



12.5



25.0



50.0



75.0

Fig. 3. A visual discrimination test with the discriminanda embedded in varying amounts of visual noise. Six pairs of X and O discriminanda are shown embedded in increasing amounts of background noise. Each number below a pair of X and O figures represents the percentage of background noise.

Once such a measurement has been obtained, one may compare a pigeon's visual capacity to filter out visual noise before and after visual system injury. One may also compare the filtering capacity of pigeons sustaining tectofugal or thalamofugal injury. A previous study of visual processing in humans (French, 1954) featured a similar technique which was successful in approximating the minimum "pattern-to-noise" ratio that permitted efficient pattern recognition.

If the principle of channel capacity holds for discriminative processing in the pigeon visual system, we can expect that significant increments in visual noise will present increasing interference in pattern discrimination in normal birds.

If the telencephalic areas of the pigeon visual system serve to filter out irrelevant information during visual discrimination, then damage to tectofugal or thalamofugal components in the telencephalon should adversely affect the filtering process such that small amounts of visual noise prohibit pattern discrimination.

EXPERIMENT I

Experiment I was designed to examine the capacity of the visual system to filter out irrelevant stimuli to perform a pattern discrimination. Experiment I tests the following hypothesis: As the amount of background noise increases, correct pattern discrimination decreases.

The pigeon visual system is assumed to have a limited capacity to efficiently filter out irrelevant stimuli, i.e., suppress noise input while processing pattern input. The channel capacity will be defined as the maximum amount of information transmitted, i.e., the maximum ability of the pigeon to discriminate the noise-embedded patterns. Since the pigeons' ability to discriminate the noise-embedded patterns will not exceed the pattern ambiguity created by the background noise, the channel capacity can be established by performing tests in which the noise suppressing capabilities are exceeded by the noise inputs. Thus, when pattern ambiguity is provided which is less than channel capacity, perfect transmission of pattern signals should result. When the pattern ambiguity exceeds the subject's discriminating ability, the amount of pattern information transmitted should remain constant. This level of stability can serve as an index of the pigeon's channel capacity for pattern-noise input.

METHOD

Subjects

Fifteen unsexed White Carneau pigeons (Columba livia) obtained from the Hillside Pigeon Farm, Hyattstown, Maryland, were used as subjects. The pigeons were 1.5 - 3 yrs of age at the start of the experiment and their free-feeding weights ranged from 450-600 g. During the experiment, the birds were maintained at 75%-80% of their free-feeding weights and water was available at all times in the home cage.

Stimuli

Fourteen pairs of embedded patterns were used in each testing session (see Fig. 3). The pattern stimuli consisted of film negatives which were prepared in the following manner. The stimulus targets, either an X or O, were constructed from black vinyl plastic letters (super stick E-Z-LETTER QUICK STIK CO.). The "noise" in the background was formed with small particles of black construction paper. Each of the target stimuli was superimposed on 50 mm squares having one of several densities of background noise: 0%, 6.25%, 12.5%, 25.0%, 50.0% and 75.0%. The percentages of background noise represent the percentage of the 50 mm square that was covered by the noise particles. Thus, 12.5% background noise means that 12.5% of the area of the display was covered by the noise particles. The squares with target

stimuli and background in place were then photographically reduced in size on F071P, Rapidoline Ortho, high-resolution, high-contrast film. The negatives were mounted on Lindia glass slides. The resultant projected image was a reversal of the original, i.e., the X and the O (both 12.5 mm high) were white and were surrounded by white noise on a black circular field (25 mm in diameter). Since both the X and the O were photographed on the same sheet of film, and were of equal area, their projected images were of equal luminance.

The slides with attached negatives were then matched for luminous flux using a Photovolt Model 520-M photometer. The luminous flux was matched to within a .01 log unit difference for all 14 stimulus pairs by adding Kodak number 96, gelatin Wratten neutral density filters.

Assuming that the pigeons viewed the stimuli at a distance of approximately 66.6 mm, which is their near-point of accommodation (Hodos, Leibowitz & Bonbright, 1976; Macko, 1978), the projected images of the stimuli subtended a visual angle of approximately 10.75° . Since the average size of the projected images of the noise particles was approximately 1.0 mm, their angular subtense was approximately 51.6 min. These values are well above the reported values for near-field visual acuity in pigeons of approximately 2.0 min of visual angle (Hodos, et al., 1976; Macko, 1978).

The contrast of the stimuli was measured by using a United Detector Technology photometer with a fiber-optic probe and pinhole aperture. The luminances of the stimuli and the dark surround were measured and the contrast of the stimuli were calculated from the formula:

$$\%C = \frac{L_T - L_S}{L_T + L_S} \times 100$$

in which %C is the contrast expressed as a percentage, L_T is the luminance of the target or noise particle and L_S is the luminance of the surround. The contrast of the stimuli ranged from 65% to 89%. The great majority of the stimuli fell in the range of 70% to 80% contrast.

Four different stimulus sets were used during the study. In each testing session, a different stimulus set was used, i.e., the same set was not used in two consecutive sessions. This procedure was employed in order to minimize the likelihood of the pigeons using extraneous stimulus properties (e.g., specific configurations of noise particles) as cues for discrimination (Banks, Bodinger & Illige, 1974; Banks & Prinzmetal, 1976).

Apparatus

The testing apparatus consisted of a 3-key Lehigh Valley Pigeon Test Chamber that had been modified to permit

illumination of the center key by an externally located slide projector. The keys were constructed of plastic Polacoat rear-projection screen and were 2.5 cm in diameter. The interior of the pigeon chamber was painted flat white and was illuminated by 2 ceiling mounted General Electric F6T5-CW-HH Fluorescent lamps. The light from the lamps was diffused by a sheet of white translucent Plexiglas.

The illumination of the test chamber and response keys was measured with a Simpson Model 408 photometer calibrated against a certified luminance standard traceable to the U.S. Bureau of Standards. The overall chamber illumination was 193.71 lx. The luminance of the walls varied from 25.0-27.5 cd/m^2 . The stimuli were projected via a Kodak Model 700 Carousel projector that had been modified for remote operation. The light source for the center key was a Sylvania DEK 500 W projection lamp. The lamp was powered through a Superior Electric voltage regulator. The current through the lamp was occasionally adjusted to maintain the luminance of the 0% noise stimulus at 23.7 cd/m^2 . The side keys were illuminated by Tung-Sol No. 1819 lamps powered from a regulated 28 V DC power supply. The left-side key luminance was 10.8 cd/m^2 and the right-side luminance was 53.8 cd/m^2 . This difference in side key luminance helped to facilitate the discrimination of the right and left side keys.

Training Procedure

First, the pigeons were rewarded with Purina Pigeon Grains for pecking each of two side keys when each was randomly illuminated. Following this, the pigeons were shaped to peck the center key 10 times when it was trans-illuminated with diffuse white light. The tenth peck on the center key darkened that key and illuminated one of the side keys. A single peck on the lighted side key resulted in illumination of the food magazine and 2-3 sec. access to mixed grains. When this stage of preliminary training was complete, the pigeons were reinforced for pecking the left-side key when the X with 0% background noise was projected on the center key and given reinforcement for right-side key pecking only when the O with 0% background noise was projected. In order to permit a large number of trials per session without satiating the pigeon, a random 50% of the correct responses were followed only by secondary reinforcement (i.e., illumination of the feeder light). The incorrect side key responses resulted in a 3.5 sec "time-out" period during which all keys were dark and pecks were ineffective. A correction procedure was used in which the trial was repeated until the bird pecked the correct key. Correction trials were not tallied and corrected responses were reinforced by the illumination of the feeder light only.

When the performance of the X and O discrimination without background noise reached 90% correct within 336 trials, psychophysical training began (see Fig. 4). A psychophysical training session commenced with two 24-trial "warm-up" periods during which the stimuli X and O without background noise were discriminated. Following the warm-up periods, another 24 trials of 0% noise stimuli were then given. If the birds' performance were 90% correct or better during this block of trials, the apparatus advanced to the psychophysical testing with variable noise backgrounds. If the subjects' performance during the assessment period were less than 90% correct (i.e., more than 2 errors), the subject received additional training on the no-noise condition for the remainder of the session, 264 trials, and the session was regarded as a training session.

If performance during the assessment was 90% correct or better, then the psychophysical testing was carried out using a variation of the method of constant stimuli. Accordingly, the data collected during the assessment period was used as the first determination of performance on X vs O with 0% noise and this period was followed by 5 24-trial blocks in which the stimuli X vs O with 6.25%, 12.50%, 25.0%, 50.0% and 75.0% noise backgrounds were presented in ascending order. Within each stimulus pair, stimulus presentation followed the Fellows sequence (1967). Following the 24 trials with 75.0%

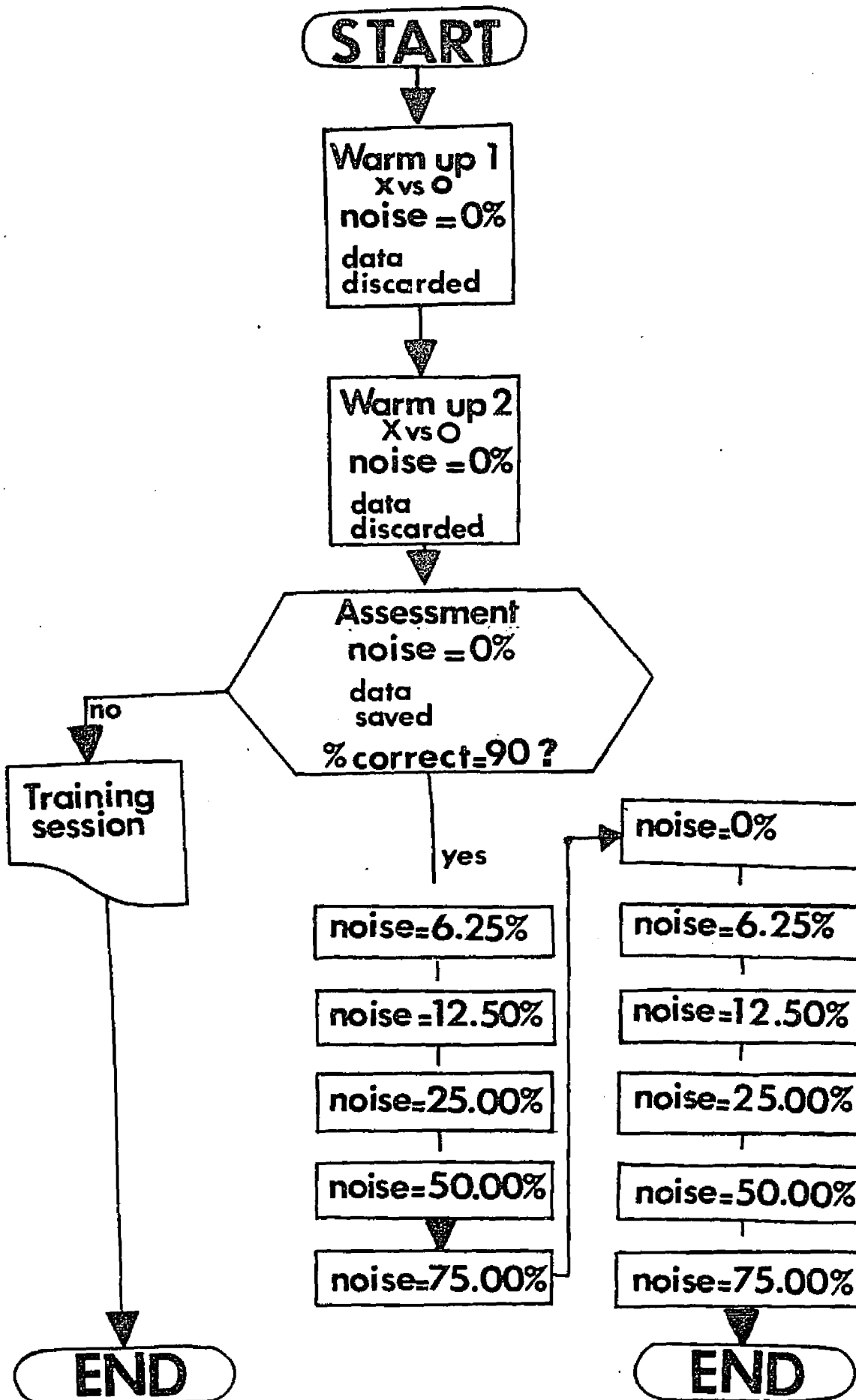


Fig. 4. A flow chart of the sequence of training and psychophysical testing procedures used to assess the visual channel capacity for noise-embedded discrimination.

background noise, the pigeon was presented with a second ascending sequence of trials. However, no assessment contingency was in effect during the second series since the decision had already been made that this was to be a psychophysical testing session.

The data collected during the first and second series of stimulus presentations were combined to form a psychometric function; i.e., the percentage correct for each stimulus pair was plotted as a function of the percentages of background noise (see Fig. 5). The value on the noise continuum that was equal to 75% correct was determined graphically (see Fig. 5) and was taken as the "noise resistance limit". Thus, the noise resistance limit is defined as the greatest amount of background noise which the bird could tolerate while discriminating X from 0 with an accuracy of 75% correct. On rare occasions, the psychometric function crossed the 75% correct line more than once. These ambiguous data were discarded.

In order to obtain data comparable to a threshold of noise tolerance, the noise resistance limit indices were subtracted from 100 to form the "noise interference index". This measure, like the difference threshold, has a high value when performance is poor and declines in value as performance improves. Thus a noise interference index of 90 would indicate that 10% background noise resulted in discrimination

D-273
session 24

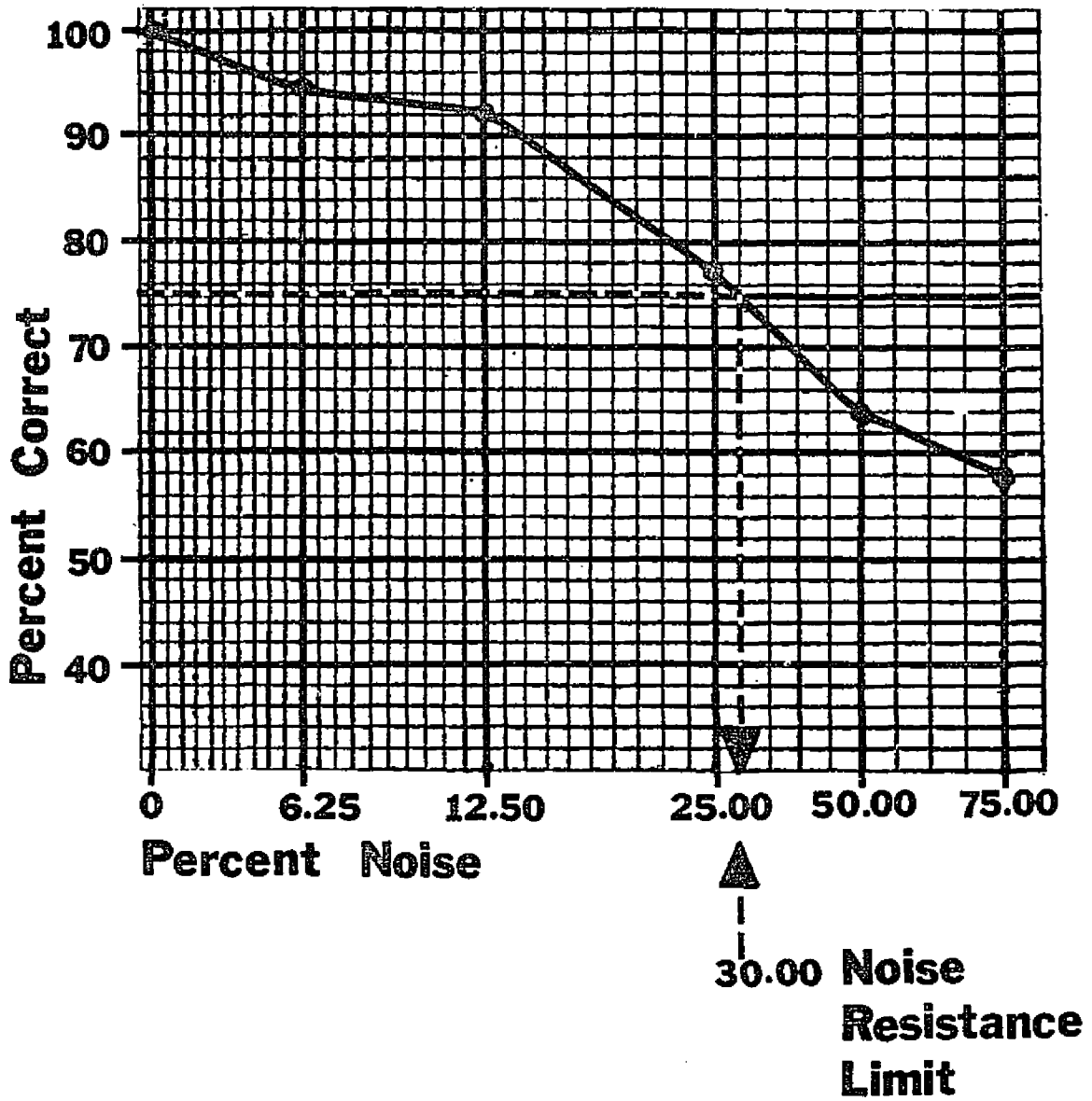


Fig. 5. An intact pigeon's psychometric function obtained during one session of noise-embedded discrimination testing. The horizontal broken line represents the 75% correct response level. The vertical broken line represents the noise resistance limit, i.e., the highest value on the noise continuum that is equal to 75% correct discriminations.

of less than 75% correct. A noise-interference index of 25 would indicate that 75% background noise did not produce a serious impairment in performance.

A daily plot of the noise interference index was carried out for each pigeon. Figure 6 presents a plot of the noise interference indexes calculated for a normal bird. This illustration shows typical progress in discriminating the test patterns in the presence of background noise. Thus, initially in training, this bird had a noise interference index in the range of 80-100, which indicates that small amounts of background noise were able to hinder that bird's discrimination performance. However, as training progressed, the interference index declined to the 30-40 range, indicating that the bird was able to perform well in the presence of considerably higher densities of background noise.

Preoperative data were collected for each bird until its performance satisfied a criterion of stability, i.e., the individual indices of noise interference did not deviate from the mean index of 5 successive sessions by more than 25%. For example, in order to be regarded as stable a mean noise interference index of 10 would have to have been obtained on 5 successive days of data yielding noise interference indexes within the range of 12.5-7.5.

D-357

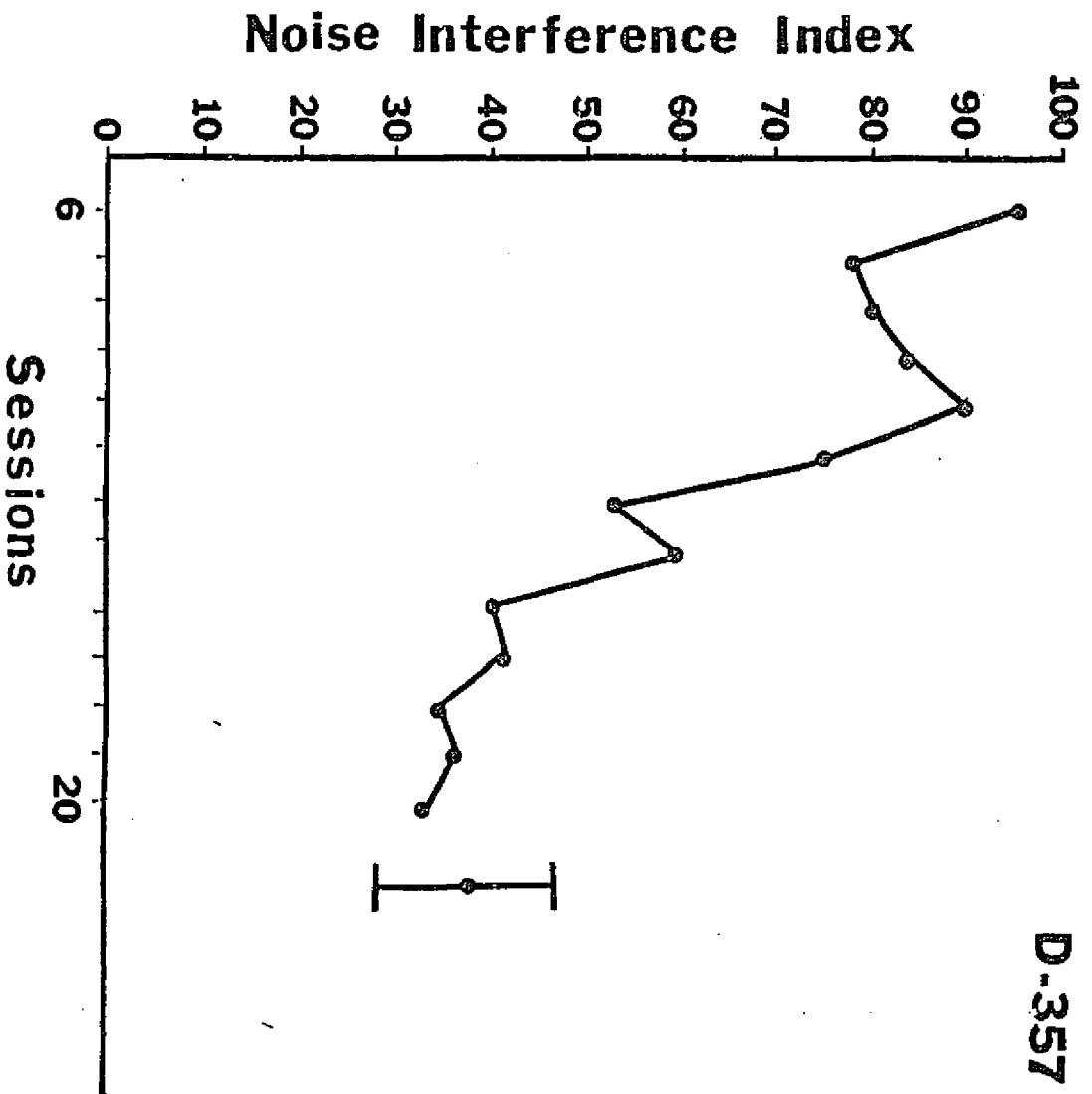


Fig. 6. A typical plot of the daily noise interference indexes calculated for an intact pigeon. Each data point represents the noise interference index as a function of test sessions. The vertical bar represents the range ($\pm 25\%$) criterion of stability limits. The point bisecting the vertical bar represents the stable mean interference index.

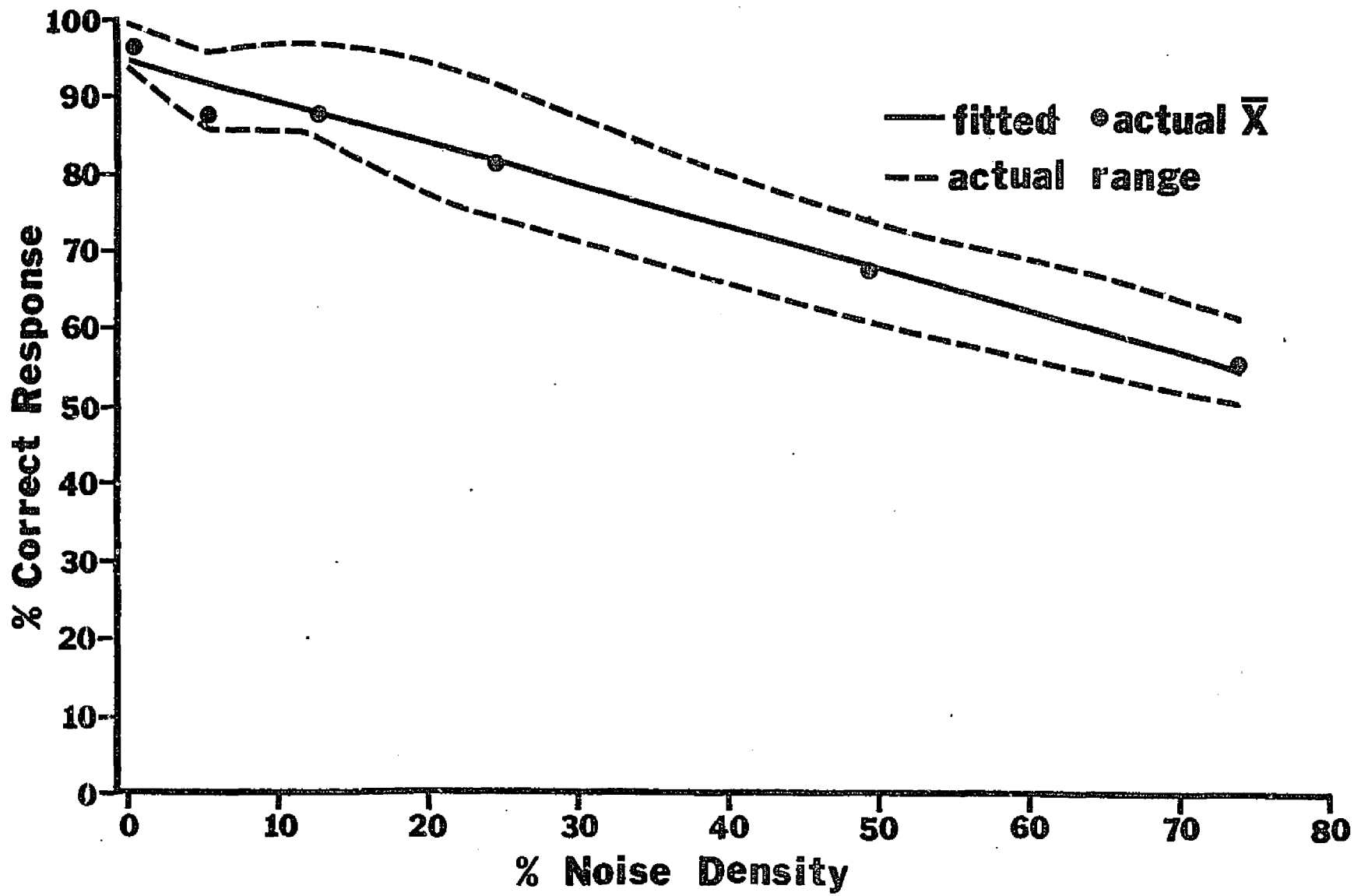
RESULTS

All subjects acquired the initial discrimination of X and O (without background noise) to a criterion of 90% correct per 336 trials in 3 to 8 training sessions. The psychophysical testing with graded noise densities was designed to test the hypothesis that significant increments in background noise would present increasing interference during pattern discrimination in normal birds. To this end, the total number of correct responses obtained at each noise level was tallied, the mean number of correct responses was computed and the data points plotted for each bird. A straight line was fitted to the data points by the method of least squares. In addition, the squared residuals were also computed for each case. As shown in Table 1, a negative linear relationship obtains in every case, i.e., for every increment in background noise there is a decrease in the percentage of correct discriminations. The exceptionally high negative correlation coefficients found between level of noise and percent of correct discriminations, as well as the small error functions (squared deviations of data points from the line of best fit) indicate that a linear equation renders an exceptionally good fit (see Table 1). Figure 7 presents a straight line fit to the pooled data for all pigeons. As can be seen, the range of deviations from the line is minimal. Thus, not only is the interference hypothesis accepted but it is con-

Table 1. THE MEAN NUMBER OF CORRECT RESPONSES GIVEN AT EACH NOISE FOR EACH SESSION

FIGURE	NOISE DENSITY												Line of Best Fit	$(Y-Y')^2$	r_{xy}
	0%	Sd	6.25%	Sd	12.50%	Sd	25.00%	Sd	50.00%	Sd	75.00%	Sd			
D-355	46.4	2.16	41.8	7.63	42.1	8.60	37.6	7.51	33.1	8.22	26.2	4.38	Y = -.24X + 44.55	7.89	-.98
D-408	45.7	2.12	40.8	7.94	41.4	7.57	37.9	7.64	32.2	8.22	27.0	4.43	Y = -.23X + 44.02	6.60	-.98
D-273	44.7	4.15	42.3	6.26	42.5	5.28	36.2	7.27	28.9	4.82	27.6	6.76	Y = -.24X + 43.95	18.22	-.96
D-414	45.8	2.53	42.9	4.38	43.3	4.39	40.2	3.67	32.0	4.60	28.6	3.93	Y = -.23X + 45.43	6.27	-.99
D-409	47.5	.71	45.8	2.41	46.1	2.02	40.8	6.45	32.9	9.35	29.0	5.09	Y = -.26X + 47.78	6.84	-.99
D-357	46.6	1.94	42.3	5.74	41.5	6.68	38.2	7.53	34.6	10.15	24.2	3.93	Y = -.26X + 45.38	12.12	-.98
D-358	46.1	2.06	40.9	4.79	40.8	5.58	37.3	8.31	33.3	7.75	26.0	3.58	Y = -.24X + 44.00	8.98	-.98
D-538	47.0	1.84	42.0	6.48	40.4	7.73	39.4	8.95	31.5	6.01	23.9	3.96	Y = -.28X + 45.31	9.69	-.99
D-405	45.2	2.86	43.4	4.38	43.5	4.22	38.9	6.86	35.1	6.79	23.9	3.80	Y = -.27X + 45.90	13.02	-.98
D-537	47.1	1.43	44.5	3.65	43.1	4.50	43.2	5.82	32.9	5.14	25.3	4.27	Y = -.29X + 47.91	10.53	-.98
D-464	45.8	2.14	43.5	5.01	41.5	5.44	41.6	5.76	30.3	4.22	24.2	3.53	Y = -.29X + 45.99	10.81	-.98
D-412	46.4	1.63	43.0	5.26	43.2	5.96	38.5	7.75	29.2	5.26	25.4	3.28	Y = -.29X + 45.72	8.90	-.99
D-410	46.0	2.72	44.1	3.05	45.0	3.13	43.9	3.32	29.9	7.73	26.8	4.23	Y = -.28X + 47.24	18.15	-.96
D-411	46.0	2.23	42.3	6.10	41.3	7.03	37.1	9.75	33.6	8.28	28.8	4.24	Y = -.21X + 44.18	6.84	-.98
D-520	47.1	1.51	45.7	3.80	45.7	3.59	43.7	6.64	38.6	7.29	26.5	2.86	Y = -.26X + 48.51	21.62	-.96

Fig. 7. A straight line fit to the percentage of correct discriminations per percentage of background noise for all intact pigeons. Each data point represents the mean number of correct responses obtained at each noise level for every intact pigeon studied. A scatter diagram of actual data points is not presented because actual deviations from the line are so small as to make them indistinguishable. Therefore, the range of actual data points is represented by the broken lines. The equation for the linear fit is $Y = -.54X + 94.42$. The correlation between the number of correct responses and the percentages of background noise is $r = -.997$. The error function $(y - \tilde{y})^2 = 7.7961$. The error function is the sum of squared deviations of data points from the line of best fit.



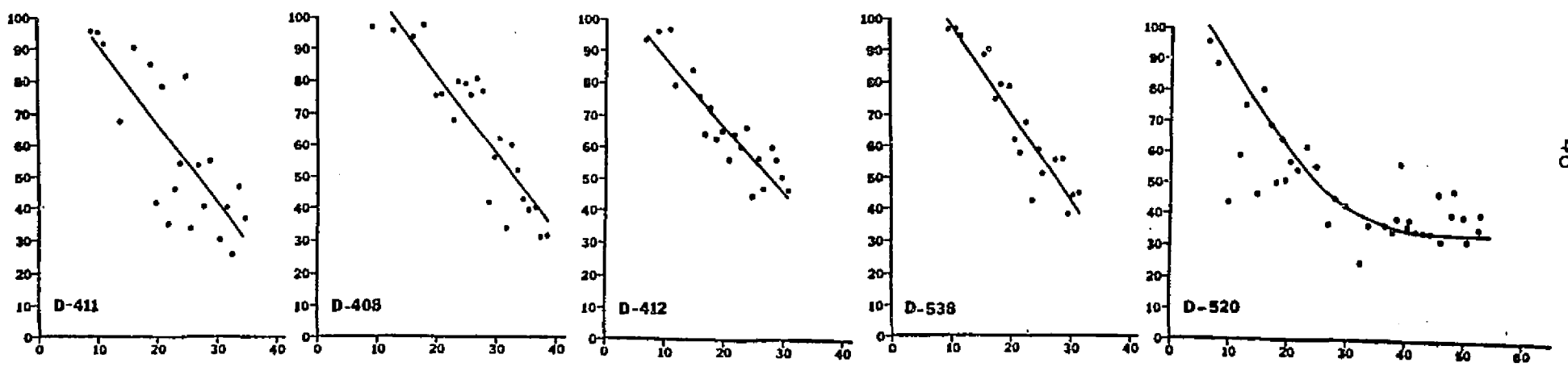
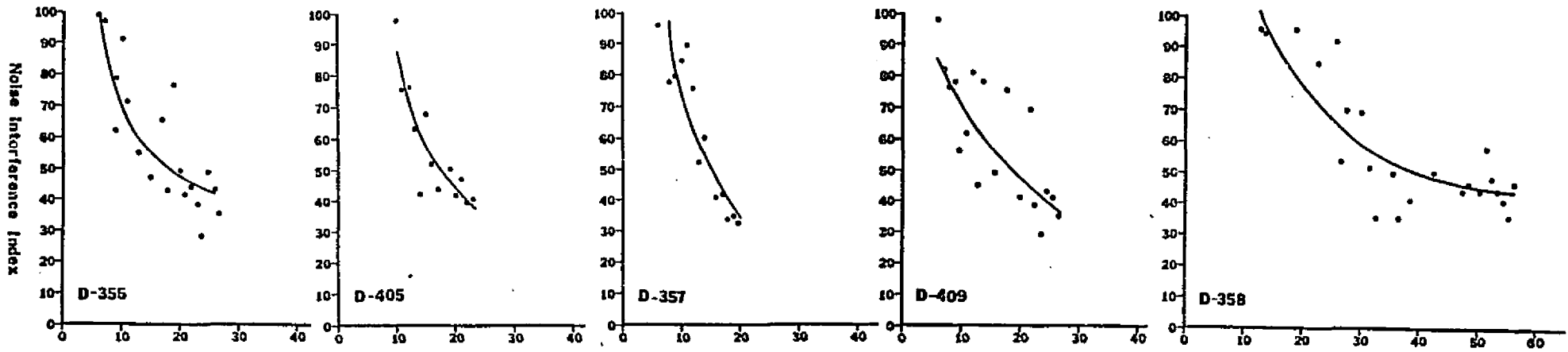
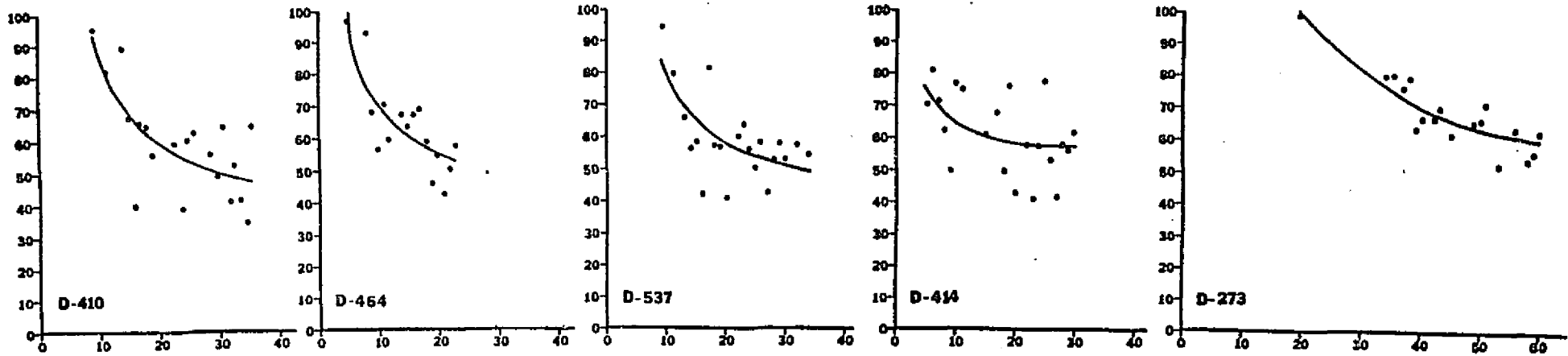
sistently verified by the homogeneous performance of the pigeons.

The total number of preoperative sessions (both training and psychophysical) required for the birds to meet the performance stability criterion ranged from 20 to 56 sessions with a mean of 32 and a standard deviation of 9. The total number of psychophysical trials required to meet the stability criterion ranged from 3,744-10,128 with a mean of 6,134 and a standard deviation of 1,789. Thus, all of the pigeons were able to perform the discrimination and eventually meet the stability criterion in spite of moderate to high levels of background noise (42.67%-63.21%). The average amount of noise that did not interfere with discrimination at the 75% correct level was 53.39% with a standard deviation of 7.44%. Hence, the pigeons' visual channel capacity to discriminate patterns was exceeded by patterns embedded in more than 63% noise. Therefore, the visual channel capacity for the pigeons in this study is limited and reaches an asymptote between noise levels of 40% and 75%.

In an attempt to discover if discrimination practice determined the amount of information which the pigeon could visually process, the mathematical relationship between the amount of practice and the degree of visual tolerance was established. Six types of curves were fitted to the noise interference index plot for each subject. Curve fitting was accomplished by computer. The six functions fitted to each bird's noise interference index function were linear, expo-

ponential, power, and three hyperbolic: $Y = A + B/X$, $Y = 1/(A + BX)$, $Y = X/(A + BX)$. Figure 8 illustrates scatter diagrams of the actual data points of each bird superimposed on the curve of best fit for that bird. As can be seen, in 10 out of 15 cases the best fitting curve was a hyperbolic function. In the remaining 5 cases the best fitting function was exponential in 1 case (D-409) and linear in the remaining 4. Thus, in most of these observations practice appears to promote the normal pigeon's tolerance of higher noise levels to a point where little or no improvement occurs; while in a few other cases, it would appear that increased practice leads to increases in discrimination efficiency at a constant rate.

Fig. 8. Curves of best fit for the noise interference function for each pigeon. Scatter diagrams of the actual points of each bird are superimposed on the curve of best fit for that bird. Equations for the curves of best fit are given in Table 4.



DISCUSSION

Experiment I examined the effects of stimulus ambiguity on pattern discrimination. Stimulus ambiguity was created by superimposing increasing percentages of experimental noise on familiar visual patterns. As expected, the greater the stimulus ambiguity, the poorer the pigeon's capacity for accurately processing noise embedded patterns (see Fig. 7). The marked negative slope of the linear function clearly indicated that the amount of background noise has a detrimental effect on the accuracy of pattern discriminations. For small percentages of background noise, the accuracy is quite high but as the percentage of noise increases there is a linear decline in the percentage of correct discriminations. Thus, noise densities in excess of 50% interfered with processing of the stimuli sufficiently to prevent discrimination at the 75% correct level (see Table 1).

This finding of a linear relationship between the amount of background noise and the ability to discriminate the embedded patterns is similar to that obtained by French (1954) in a study of human visual processing. French studied pattern recognition as a function of both the number of dots comprising the pattern's surround and the number of dots constituting the pattern. A positive correlation was found between an increase in density of the dotted noise background and an increase in errors of pattern recognition. Similar results

have been reported in visual masking studies (Uttal, et al., 1970; Levine & Mayzner, 1976; Bjork & Murray, 1977).

The linear functions found in this study also support what has been described as the "display size effect", a result commonly found in signal-detection experiments (Estes & Taylor, 1976). The display size effect is one in which detection of a stimulus target decreases as the number of noise elements in the stimulus display increases.

Individual differences appeared in the limits of discriminative capacity when visual noise was introduced. These differences are reflected in the wide range of noise interference indexes obtained (57.33-36.79) which represent the highest levels of visual noise that intact pigeons can tolerate while discriminating X from O.

Practice in discriminating noise-embedded patterns can improve noise tolerance. In 10 out of 15 cases, a hyperbolic equation best described the functional relationship of the noise interference index over sessions. These data indicate that in most cases, the noise interference index could be decreased with practice, until the higher percentages of noise imposed a physical restriction on the discrimination of the patterns. This finding is similar to that of Rambo and Johnson (1964) who studied the functional relationship of practice effects and adaptation level (AL), an index which also accounts for the alterations in stimulus judgments that

result from changes in stimulus context (Helson, 1964). Rambo and Johnson plotted AL estimates from human judgments of numerosness of dots over a series of 45 trials and determined equations which reflected the change in AL with practice. They found that a hyperbolic equation best described the effects of practice on AL. Thus, like the adaptation level, the index of noise tolerance varies with practice but then shifts to a stable level very rapidly during the very early sessions. This result is important for it demonstrates that although practice succeeds in increasing the capacity to discriminate noise-embedded patterns, it does so within limits. Thus, the range of discriminative ability can be quantitatively stated with a psychophysical measure of noise embedded pattern discrimination is employed.

Occasionally, rectilinear psychometric functions are obtained in experiments on sensory discrimination. The same is true of this experiment where 4 out of 15 cases showed a linear regression of the noise interference index over sessions. A possible explanation of the linear functions demonstrated by pigeons D-408, D-411, D-412 and D-538 is that the functions are incomplete, i.e., the psychophysical training was not given long enough for the interference functions to bottom out.

There is another explanation however. Perhaps these pigeons were able to obtain sensory evidence (e.g., constant differences in the pattern features) which allowed them to unambiguously choose the correct response; i.e., those pigeons with linear functions might have been able to reject a proportion of noise as being signal on the basis of pattern features learned with repeated exposures, e.g., the presence of the open center in the O pattern vs the absence of the open center in the X pattern. Some results of signal-detection studies support this conjecture. Swets, Tanner and Birdsall (1961) conducted a forced choice signal detection task in which second choices were permitted if an observer did not make a correct selection on his first attempt. Swets and colleagues found that second choices show better than chance discrimination. Similarly, Brown (1964; 1965) found that second choices in learning experiments are not random, but are based on information about the correct response.

Whether the functional relationship of practice to noise-embedded pattern discrimination is hyperbolic or linear, Experiment I has shown that there is a physical limit in the amount of noise the visual system can suppress while processing pattern input. This finding underscores the appropriateness of applying the concept of limited channel capacity to the visual processing of noise-embedded patterns.

Undoubtedly, the spatial interaction of pattern and noise led to performance deficits in the present experiment. Performance deficits on visual-signal-detection tasks have been shown to vary as a function of the spatial interaction of the visual noise with the target stimuli (Bjork & Murray, 1977). Additionally, there is evidence to suggest that the noise elements in a display adversely affect signal detection by creating confusion between signal and noise either by perceptual grouping of the stimulus target with the noise (Banks & Prinzmetal, 1976), by the degree of similarity of signal to noise (Bjork & Murray, 1977) or the proximity of signal to noise (Bjork & Murray, 1977). Likewise, deficits in noise-embedded pattern discrimination became evident in the present experiment when an increase in the density of noise backgrounds impoverished the visibility of the pattern stimuli via spatial interaction.

Intriguing, however, is the prospect that the degree of performance deficit varied as a function of the decreased lateral inhibition resulting from too much spatial interaction. Lateral inhibition, a type of response inhibition is due to an interactive response to stimulation manifested by contiguous neural elements at all levels of the visual system (e.g., Kuffler, 1953; Baumgartner & Hakas, 1959). Supposedly, the lateral inhibitory mechanisms which are operative in cortical neurons that are sensitive to specific stimulus

features (e.g., orientation, contour) enhance the contrast between the optimum stimulus and its background (e.g., Ratliff, 1961). MacKay (1973) suggests that visual systems may also have visual units which are sensitive to the texture density of visual stimuli and that these units may be capable of a gradient enhancing process. That is, the inhibition between units which respond maximally to the density of visual stimuli operates to enhance local density gradients (e.g., the edge between two surfaces of different material, or the edge between the solid X pattern and the stippled static noise background). In support of this conjecture, recent examples of response inhibition induced by visual noise have been observed in avian tectal units. In a study by Frost (1978), tectal neurons which normally responded to moving circles of light were inhibited by separate stippled background patterns which were simultaneously moved in the same direction. This situation is similar to the static pattern-noise presentations used in the present experiment. Thus, interactive inhibition may have been the primary mechanism that determined the visual channel capacity for processing noise-embedded patterns, or put another way, the minimum pattern-to-noise ratio the avian visual system could efficiently process. Conversely, once the channel capacity for noise-embedded discrimination had been exceeded by high noise levels, a decreased ability to process patterns embedded in dense noise fields may have been

due to an absence of interactive inhibition. That is, heavy densities of visual noise could have obscured or flattened the spatial gradients between the pattern and noise elements and thus suppressed the inhibitory mechanisms of "density specific" units.

EXPERIMENT II

Experiment II investigates the effects of ectostriatal and visual wulst lesions on the discrimination of the same noise-embedded patterns used in Experiment I.

If telencephalic components of the visual system act as filters that attenuate background noise during visual discrimination, then disruption of either the ectostriatum or visual wulst should succeed in increasing the load, via internal noise, on the limited channel capacity for noise-embedded pattern discrimination. Hence, we may expect pattern-noise inputs which are lower than those preoperatively tolerated to prohibit noise-embedded pattern discrimination after telencephalic damage.

METHOD

Surgical Procedure

Within 24-72 hrs. of satisfying the stability criterion, the pigeons were anesthetized via inhalation of a mixture of methoxyflurane, 95% oxygen and 5% carbon dioxide or by intramuscular injection of Ketamine and secured firmly in a Kopf stereotaxic instrument with pigeon adapters (Karten & Hodos, 1967). The site of incision was infiltrated with Xylocaine to permit wound closure under reduced general anesthesia. The cranium was exposed and the area bordering the intended cortical exposure was marked. Craniectomy was accomplished using a gas-turbine dental drill with the visual aid of an operating microscope.

Bilateral, anodal electrolytic lesions were made in the ectostriatum, visual wulst, and caudal neostriatum with size 00 stainless steel insect pins insulated except for 3, 5 or 9 mm at the tip. The electrode with 3 mm of the tip exposed was inserted horizontally into the ectostriatum. A total destruction of the ectostriatum was attempted by passing 2.5 mA of current for 20 sec at 3 points along the extent of the ectostriatum at depths indicated by the Karten and Hodos pigeon atlas (1967): A 8.8, 9.6, 10.4; L 3.8, 4.2, 4.0; V 10.2, 10.0, 9.6. The 5 mm and 9 mm tip electrodes were directed towards the visual wulst in the parasagittal plane. Both electrodes were inserted at angles oblique to the cortical

surface (60° - 5 mm tip, 43° - 9 mm tip). A total destruction of the visual wulst was attempted by passing 3 mA of current for 10 sec at 5 points along the lateral and vertical planes at depths indicated by the pigeon atlas: A 13.5; L 1.5, 2.0, 2.5, 3.5, 4.0; V 9.2, 10.3, 11.1, 10.5, 11.2. Horizontal and oblique electrode approaches were used in order to selectively destroy the ectostriate nucleus or the visual wulst laminae without disrupting the ventral hyperstriate lamina which adjoins both ectostriatum and visual wulst. Bilateral control lesions were made in the caudal neostriatum using the 3 mm tip electrode aimed vertically in the caudal neostriatum at depths: A 5.4, 4.6, 3.8; L 4.5, 5.0; V 11.0.

Postoperative Retesting

After 7 days of postoperative recovery, discrimination testing was resumed using the same preoperative procedures. Postoperative training was continued until the stability criterion was met or until the number of postoperative sessions matched the number of sessions the subjects required to stabilize their preoperative performance.

One pigeon served as an unoperated control. After a stable noise-interference index had been obtained, this unoperated pigeon was retested after a three-week hiatus.

Histological Procedure

When the post-operative behavioral assessment was completed, the pigeons were deeply anesthetized with sodium pentobarbital and subjected to cardiac perfusion via the left ventricle with normal saline followed by Heidenhain's solution (without mercuric chloride). After perfusion the bird was decapitated and the calvarium was removed to expose the brain. The head was submerged in Heidenhain's solution for 24 hrs. before transferring it to 10% formol-saline for additional fixation. After 1-3 weeks, the head was removed from the fixative, placed in the stereotaxic instrument, and blocked in situ in the transverse or sagittal plane with a scalpel blade mounted in an electrode carrier as described by Karten and Hodos (1967). The blocked tissue was then removed from the skull and allowed to fix in formol-saline for several more days. After fixation was complete, the tissue block was dehydrated in graded concentrations of ethanol, cleared in cedarwood oil, and embedded in paraffin. The paraffinized tissue was sectioned on a rotary microtome at 10 μ m in the transverse or sagittal plane. Sections of the ectostriatum cases were made in the transverse plane because the ectostriatal boundaries are more obvious when viewed transversely. Sagittal sections were taken in the visual wulst because the boundaries of the visual wulst are most easily visualized in that plane of section. Every tenth

section was mounted and stained for cells and myelinated fibers according to a modification of the Klüver-Berrera method (1953). The sectioned brains were examined using a Leitz Makropromar projector. The lesions were then reconstructed and transferred onto standard drawings of transverse or sagittal sections through an intact brain derived from the Karten and Hodos atlas (1967). Each brain was also examined microscopically for areas of necrosis. In addition, indications of gliosis, retrograde chromatolysis, cell loss and demyelination were recorded. The lesion reconstructions were then used to estimate the volume of damaged tissue by superimposing a translucent millimeter square grid over each reconstruction and measuring the area of necrosis. The areas were then summed across plates and the volume of the lesion calculated by the following formula:

$$V = \left(\frac{\Sigma A}{M^2} \right) I \text{ , in which}$$

V = volume in mm³

A = area in mm²

I = interval in mm

M = linear magnification factor,

(M² = areal magnification factor)

Since the lesions were reconstructed onto plates representing uniformly spaced sections through an intact, unprocessed brain, no correction for shrinkage is necessary.

RESULTS

Histological Results

Anatomical data are presented for all but 2 subjects, one of which served as an unoperated control and the other whose brain was inadvertently damaged during histological processing.

A microscopic examination of the remaining 13 cases revealed 4 types of lesions: bilateral ectostriate lesions (4 cases), bilateral visual wulst lesions (3 cases), bilateral caudal neostriatum lesions (2 cases), and mixed lesions (4 cases). This latter group is comprised of cases which were intended to be visual wulst lesion cases. However, the actual lesions proved to be either too extensive (including both ventral hyperstriatum and ectostriatum) or insufficiently extensive (deafferenting the visual wulst but restricted to the ventral hyperstriatum). Photomicrographs, representative of each lesion group, are shown in Figures 11, 15, 17 & 20. Reconstructions of the extent of each lesion and the accompanying cellular degeneration are shown on cross sections derived from the pigeon atlas in Figures 9, 13, 16, 18 & 19. Solid black regions represent the boundaries of necrotic tissue while stippled areas indicate the extent of chromatolytic changes. The resultant retrograde degeneration of cells in the thalamus (stippled zones) are shown in Figures 12 & 21. Table 2 gives the percentage of the total

Table 2. PERCENTAGES OF THE TELENCEPHALON THAT WERE DESTROYED

Lesion Group	Pigeon	Total Telen- cephalon**	Ecto- striatum		Ventral Hyper- striatum		Visual Wulst		Caudal Neostriatum	
			L	R	L	R	L	R	L	R
ECTOSTRIATUM	D-355	6	87	100	2	0	0	0	0	0
	D-408	2	41	24	1	0	0	0	0	0
	D-273	4	43	42	0	0	0	0	0	0
	D-414	3	22	3	0	0	0	0	0	0
VISUAL WULST	D-358	10	0	0	23	29	77	36	0	0
	D-520	7	0	0	1	17	74	82	0	0
	D-537	2	0	0	0	0	51	76	0	0
CAUDAL NEOSTRIATUM	D-464	1	0	0	0	0	0	0	9	14
	D-412	4	0	0	0	0	0	0	35	19
MIXED LESIONS	D-357	24	0	8	46	72	94	100	0	0
	D-409	11	27	0	42	17	78	32	0	0
	D-405	6	0	0	20	18	2*	0*	0	0
	D-538	4	0	0	20	12	0*	0*	0	0

*Ascending fibers from thalamus are interrupted.

**Includes damage to structures listed in table as well as injury to remaining structures of the telencephalon.

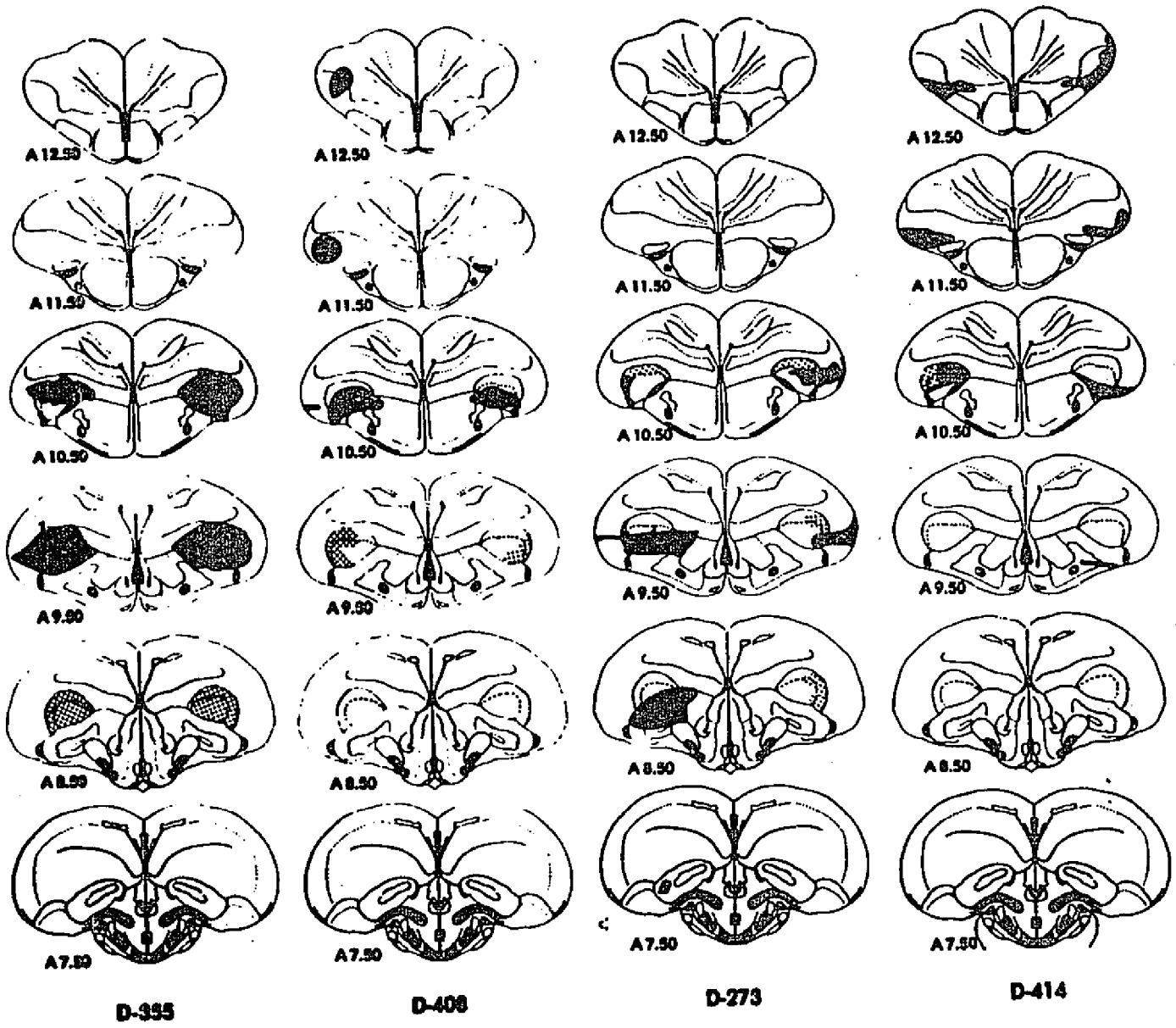
volume of the telencephalon that sustained damage and the percentages of various components that were destroyed. In the following anatomical descriptions of lesions, slight damage will refer to injury less than 30% of the total bilateral volume of a given structure. Moderate will describe 30%-50% destruction of the total bilateral volume and extensive will indicate lesions involving 50%-100% of the total bilateral volume.

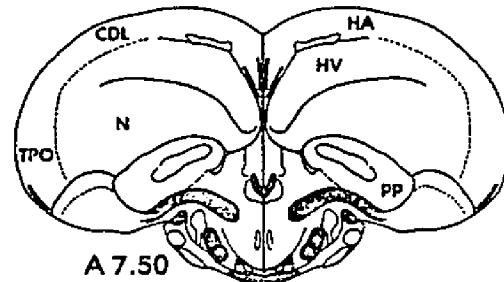
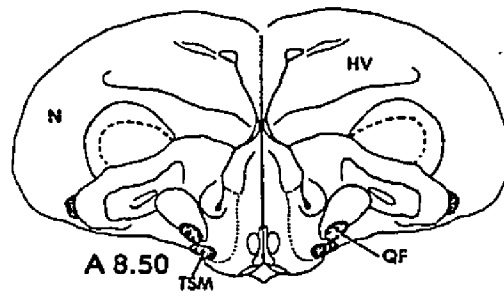
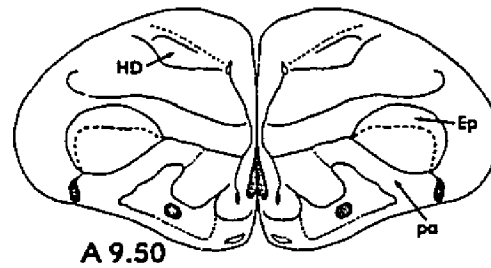
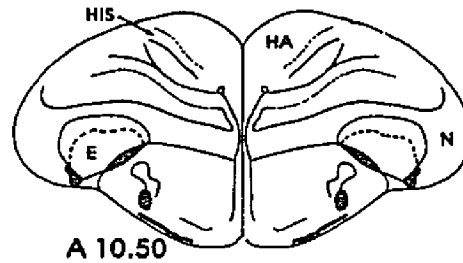
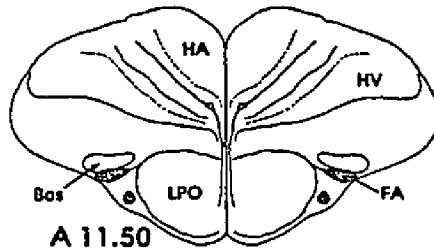
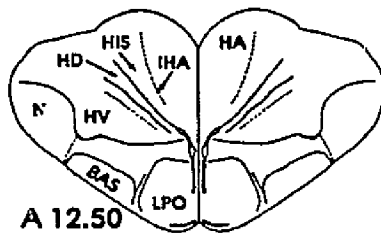
Ectostriatum Lesions

Pigeon D-355 (Fig. 9) sustained an almost complete and symmetrical ablation of ectostriate tissue. As shown in the accompanying photomicrograph (Fig. 11) the injury was generally restricted to ectostriatum with only a slight invasion of the adjoining neostriatum and paleostriatum. A small circumscribed area of cell loss was also apparent unilaterally in the ventral hyperstriatum. This appeared to result from an infarct which occurred at the dorsal boundary of the periectostriatal belt. Bilateral retrograde degeneration of the nucleus rotundus in the thalamus was complete (Fig. 12).

Pigeon D-408 (Fig. 9) suffered a moderate lesion of ectostriatum accompanied by a very slight invasion of ventral hyperstriatum, lateral neostriatum, and paleostriatum. Although the lesion in ectostriatum proper was not extensive, the injury succeeded in transecting the thalamostriate tract

Fig. 9. Reconstructions of bilateral lesions in the ectostriatum (E) onto standard brain charts derived from the pigeon atlas (Karten & Hodos, 1967). Black areas indicate zones of necrosis. Stippled areas indicate regions of cell loss.

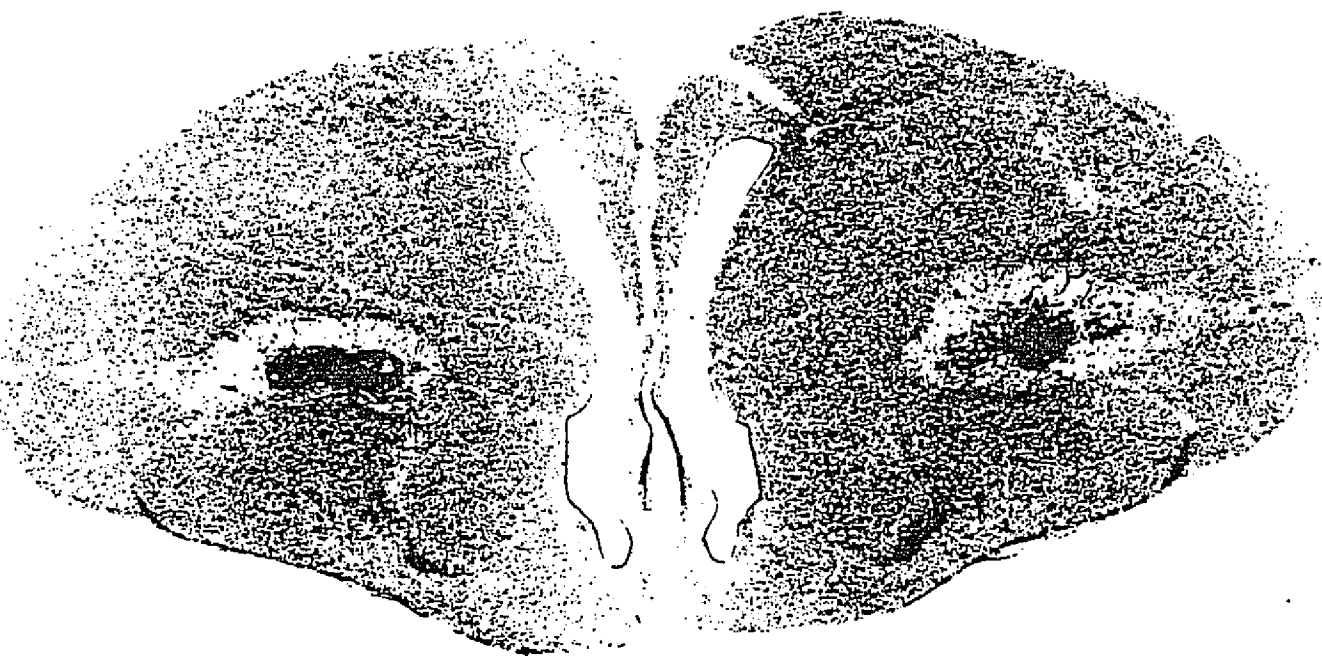




Key

Fig. 10. A key of telencephalic structures of the intact pigeon brain when viewed transversely. Cell groups and fiber tracts are identified by the following abbreviations:

Bas, nucleus basalis
CDL, area corticoidea dorsolateralis
E, ectostriatum (core region)
Ep, ectostriatum (peri-ectostriatal belt)
FA, tractus fronto-archistriatalis
HA, hyperstriatum accessorium
IHA, nucleus intercalatus hyperstriati accessorii
HD, hyperstriatum dorsale
HIS, hyperstriatum intercalatus suprema
HV, hyperstriatum ventrale
LPO, lobus parolfactorius
N, neostriatum
Pa, paleostriatum accessorium
Pp, paleostriatum primitivum
Qf, tractus quinto frontalis
TPO, area temporo-parieto-occipitalis
TSM, tractus septomesencephalicus

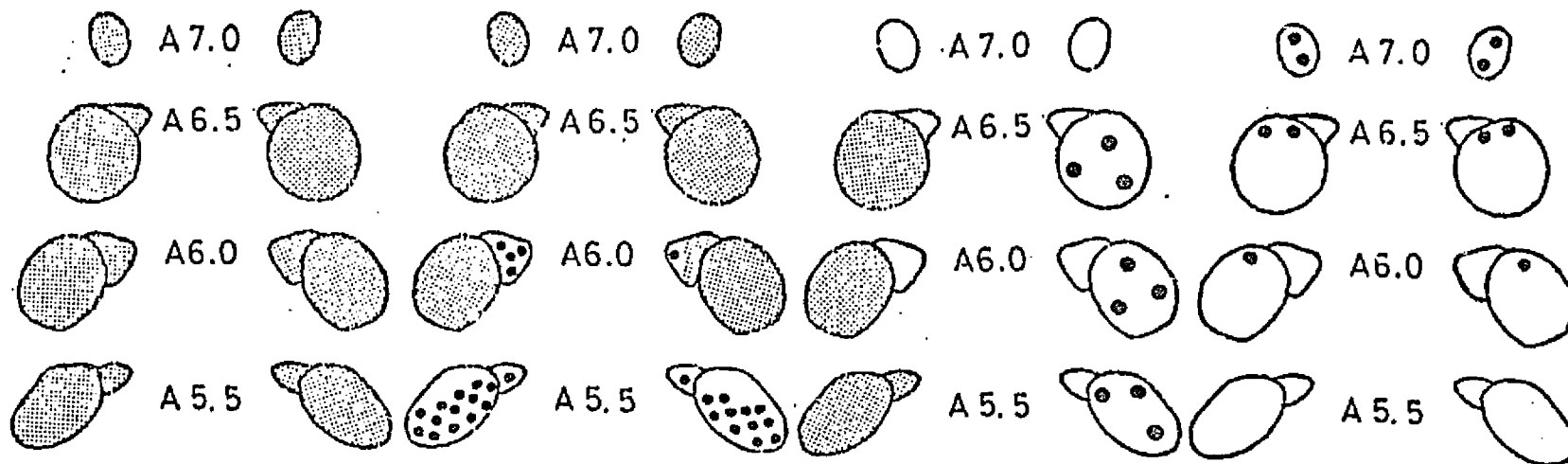


D-355

Fig. 11. A microphotograph of an almost complete bilateral destruction of the ectostriatum. The lesion is shown near the level of its maximal volume between stereotaxic levels A. 10.50 and A. 9.50 according to the pigeon atlas (Karten & Hodos, 1967).

(Magnification 10X)

Fig. 12. Transverse plane reconstructions of the extent of retrograde degeneration in nucleus rotundus following damage to ectostriatum. The number next to each section indicates the plate in the Karten and Hodos, 1967, atlas from which the drawings were derived.



D-355

D-408

D-273

D-414

●● Occasional chromatolytic cells

●● Considerable chromatolysis
with some cell loss

■ Extensive cell loss, chromatolysis

which is comprised of fibers ascending from nucleus rotundus to ectostriatum. Fiber tract transections are made obvious by the Klüver-Berrera method which permits the tracing of damaged and degenerated myelinated pathways due to their lack of myelin staining. Extensive bilateral retrograde degeneration was apparent in nucleus rotundus (Fig. 12).

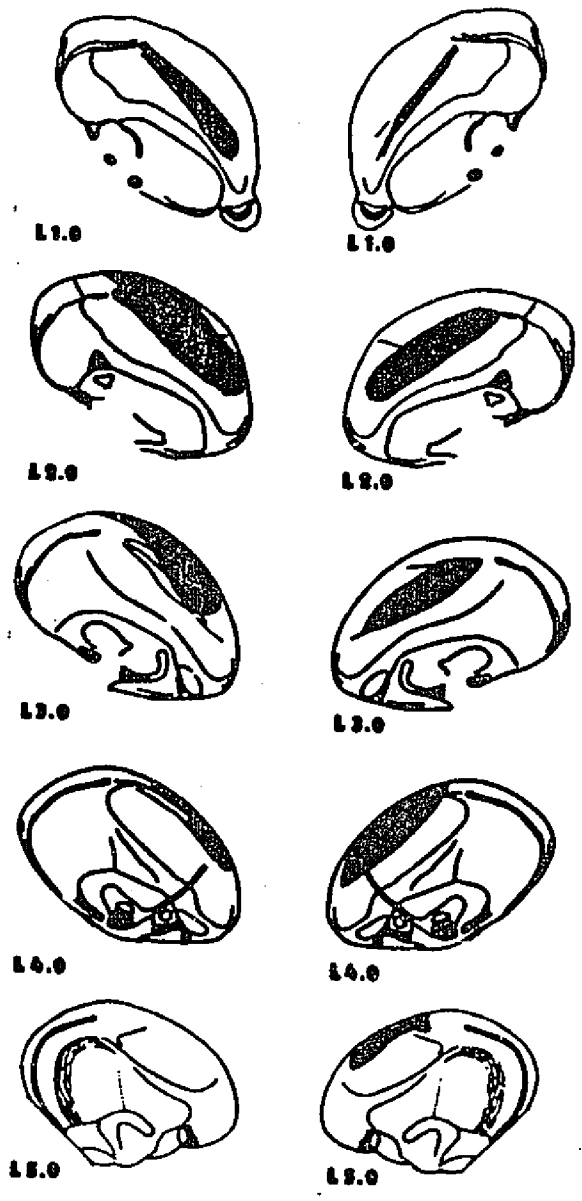
In pigeon D-273 (Fig. 9) necrosis was found in a moderate portion of the ectostriatum. However, the area of direct assault was somewhat unilateral resulting in extensive rotundal degeneration on one side only. Rotundal degeneration on the opposite side was slight as reflected by a few scattered chromatolytic cells (Fig. 12).

Pigeon D-414 (Fig. 9) sustained a comparatively small bilateral injury of the ectostriatum with destruction of the anterior ectostriatal pole on one side accompanied by light rotundal degeneration on the same side. On the contralateral side, the Klüver-Berrera method of staining revealed a minimal invasion of the thalamostriate tract where it terminates in ectostriatum. This damage resulted in light degeneration of the anterior pole of rotundus on that side (Fig. 12).

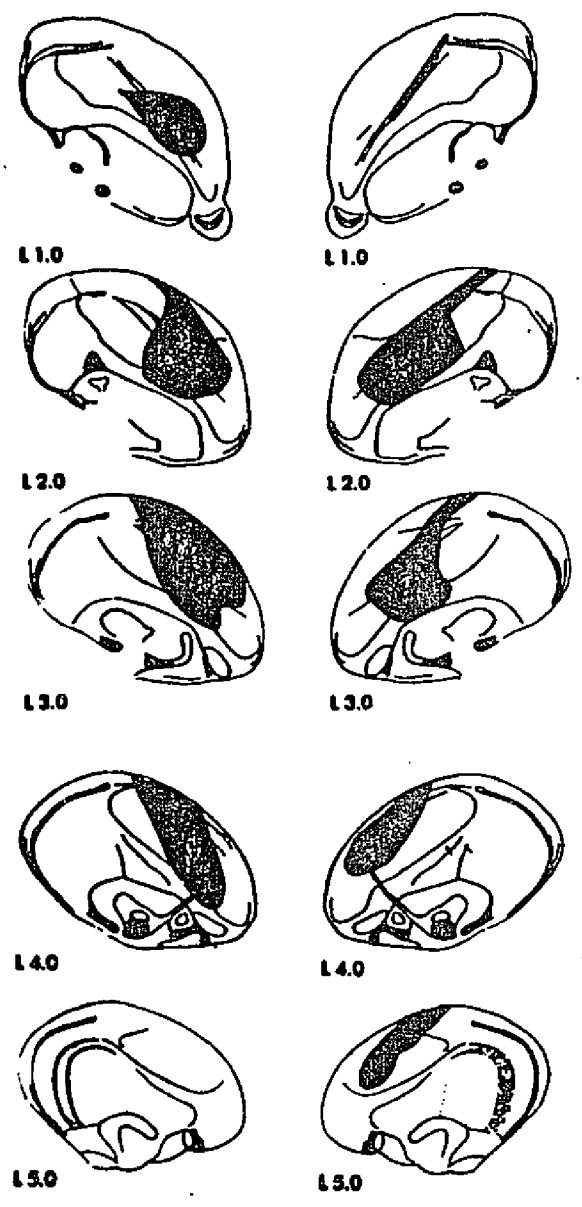
Visual Wulst Lesions

Pigeon D-358 sustained moderate to extensive damage of all components of the visual wulst (Fig. 13). The tract of fibers ascending from the principal optic nucleus to the

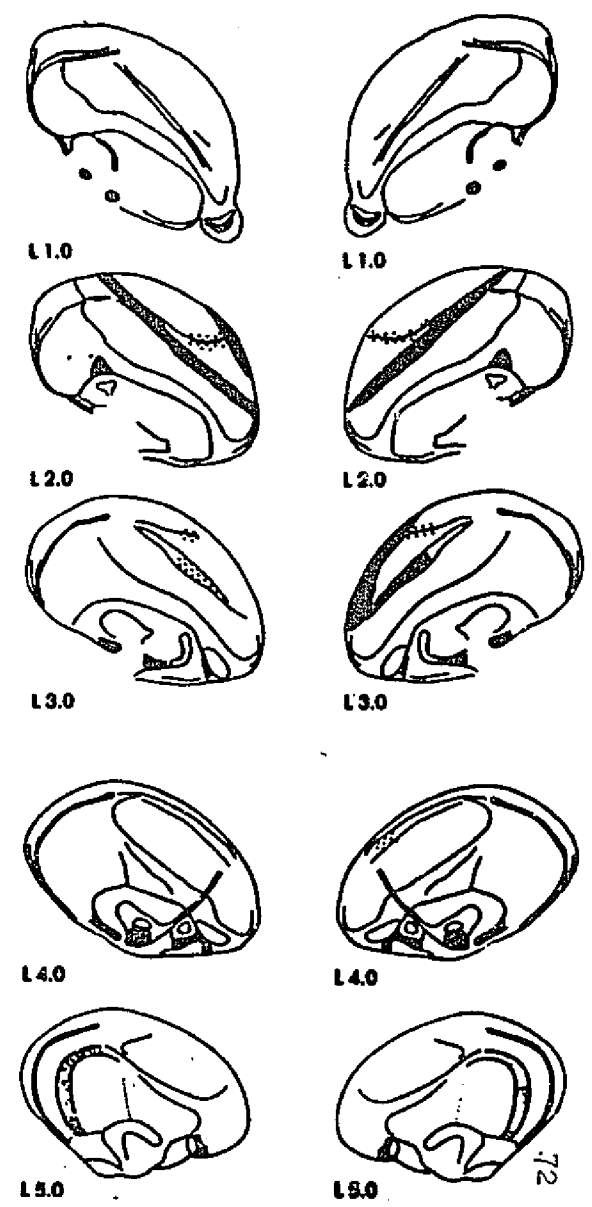
Fig. 13. Parasagittal plane reconstructions of bilateral lesions in the visual wulst (IHA and HD) onto brain charts derived from the pigeon atlas (Karten & Hodos, 1967). Black areas indicate zones of necrosis. Stippled areas indicate regions of cell loss.



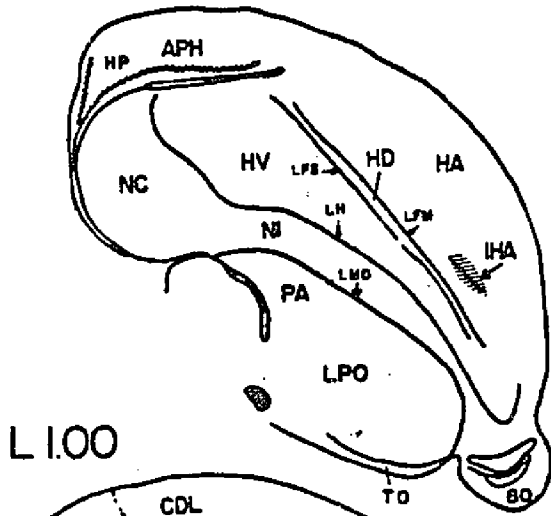
D-520



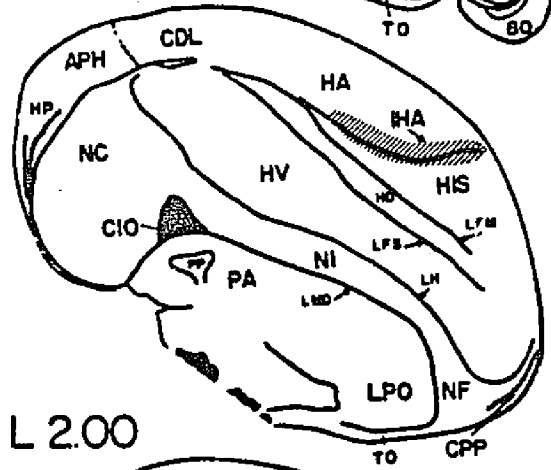
D-358



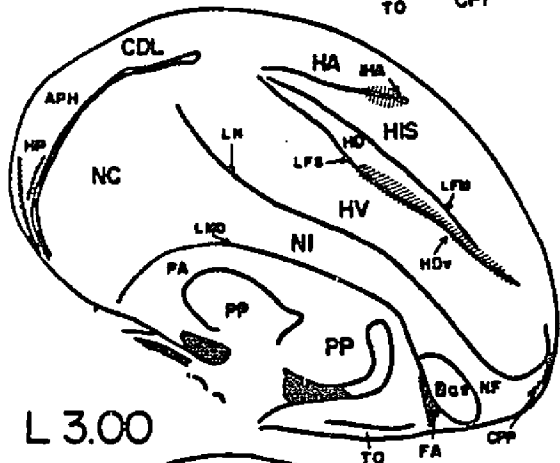
D-537



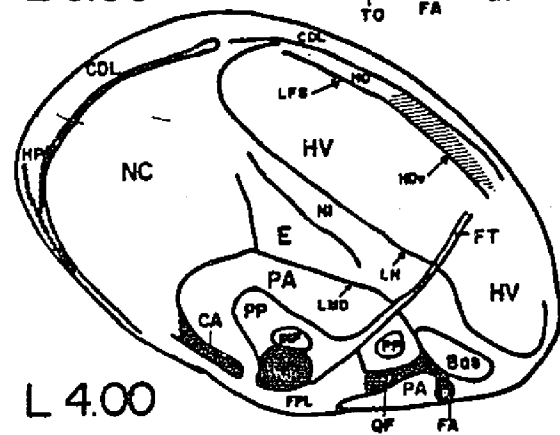
L 1.00



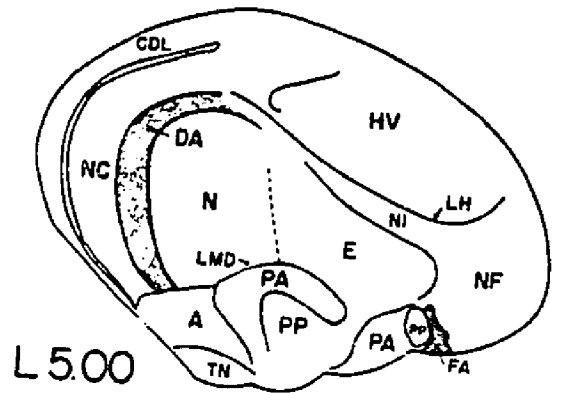
L 2.00



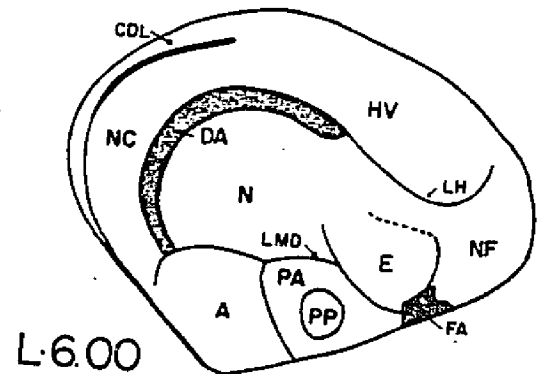
L 3.00



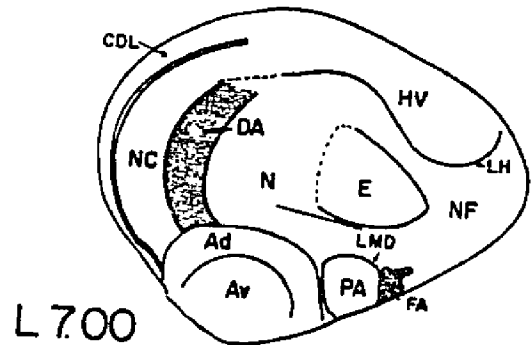
L 4.00



L 5.00



L 6.00



L 7.00

Fig. 14. A key to structures shown in sagittal sections through the pigeon telencephalon. The number next to each section indicates the plate in the Karten and Hodos, 1967, atlas from which the drawings were derived. Hatchings indicate projection fields of the OPT complex within IHA and HD. A number of cell groups and fiber bundles are identified by abbreviations:

- A, archistriatum
- Ad, archistriatum, pars dorsalis
- Av, archistriatum, pars ventralis
- APH, area corticoidea dorsolateralis
- CA, commissura anterior
- CIO, capsula interna occipitalis
- CPP, cortex prepyformis
- DA, tractus archistriatis dorsalis
- E, ectostriatum
- Ft, tractus frontothalamicus et thalamofrontalis
- HA, hyperstriatum accessorium
- HD, hyperstriatum dorsale
- HDv, hyperstriatum dorsale (visual)
- HIS, hyperstriatum intercalatus suprema
- HP, hippocampus
- HV, hyperstriatum ventrale
- IHA, nucleus intercalatus hyperstriati accessorii
- INP, nucleus intrapeduncularis
- LFM, lamina frontalis suprema
- LFS, lamina frontalis superior
- IH, lamina hyperstriatica
- LMD, lamina medullaris dorsalis
- LPO, lobus parolfactorius

NC, neostriatum caudale
NF, neostriatum frontale
NI, neostriatum intermedium
PA, paleostriatum augmentatum
PP, paleostriatum primitivum
QF, tractus quintofrontalis
TO, tuberculum olfactorium
TN, nucleus taeniae

Fig. 15. A microphotograph of an almost complete bilateral destruction of the granular visual wulst (IHA and HD). The lesion is shown at the level of its maximal volume between stereotaxic levels L. 2.00 and L. 3.00.

(Magnification 10X)



D-537

visual wulst was transected by the lesion. Only slight to moderate damage was apparent in adjoining areas of the ventral hyperstriatum.

Pigeon D-537 presented lesions which were restricted to the visual wulst proper (Fig. 13). The photomicrograph (Fig. 15) shows that moderate to extensive lesions were manifested bilaterally in the lateral division of the dorsal hyperstriatum. Extensive cell loss was apparent in most portions of the nucleus intercalatus hyperstriatum accessories (IHA). Fibers ascending from the principal optic nucleus to the visual wulst were completely demyelinated.

Pigeon D-520 (Fig. 13) suffered extensive bilateral lesions in all components of the visual wulst. The fibers ascending from the principal optic nucleus to the visual wulst were transected by the lesions. Only slight damage was apparent in the ventral hyperstriate area that adjoins the visual wulst laminae.

No unequivocal retrograde degeneration in the OPT was observed in any of those cases presenting visual wulst assault. This finding is consistent with those of Powell and Cowan (1961) who noted no retrograde degeneration of OPT except after hemispherectomies.

Control Lesions

Pigeons D-464 and D-412 manifested lesions which were restricted to the caudal pole of the neostriatum (Fig. 16). Pigeon D-464 sustained a very slight lesion which transected

the dorsal archistriatal tract on one side. Pigeon D-412 suffered a moderate sized lesion which bilaterally transected the dorsal archistriatal tract (see Photomicrograph, Fig. 17).

Mixed Lesions

Pigeon D-409 (see Photomicrograph, Fig. 20) presented a small, unilateral invasion of ectostriatum as well as considerable bilateral damage to the ventral hyperstriatum and extensive damage to bilateral areas of the visual wulst (Fig. 18). Moderate to light rotundal degeneration was found ipsilateral to the ectostriatal invasion (Fig. 19).

In pigeon D-357 comparable damage was found except that the unilateral invasion of ectostriatum was minimal with little or no signs of chromatolytic cells in rotundus (Fig. 19). Bilateral damage to the ventral hyperstriatum was also considerable in this case as was wulst ablation which was almost total (Fig. 18).

Case D-405 suffered only a slight, unilateral invasion of visual wulst and only slight damage to the ventral hyperstriatum (Fig. 21). However, the visual wulst was deafferented bilaterally by transection of the fronto-thalamic tract which contains fibers ascending from OPT to the visual wulst. D-405 also sustained slight damage to those portions of the

Fig. 16. Reconstructions of bilateral control lesions through the caudal neostriatum (NC, see sagittal key in Fig. 14). Numbers below sections indicate the stereotaxic level (Karten & Hodos, 1967) at which the lesion was made. Black areas indicate zones of necrosis.



L2.0



L2.0



L2.0



L2.0



L3.0



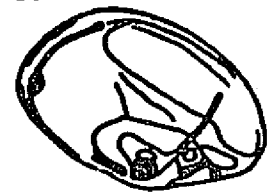
L3.0



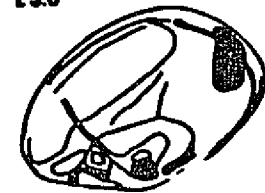
L3.0



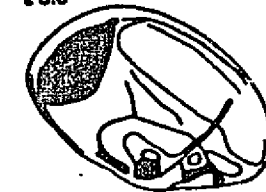
L3.0



L4.0



L4.0



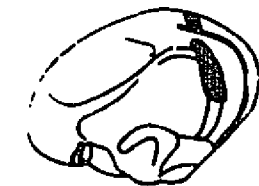
L4.0



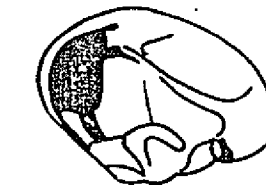
L4.0



L5.0



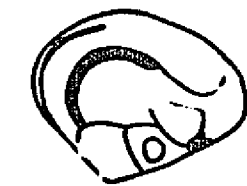
L5.0



L5.0



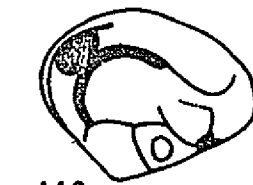
L5.0



L6.0



L6.0



L6.0



L6.0

D-464

D-412

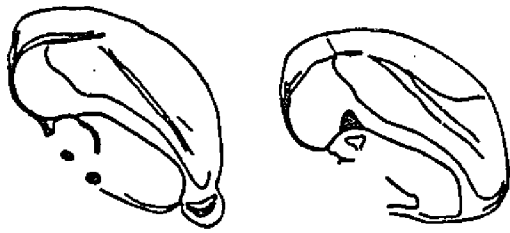
Fig. 17. A microphotograph of a moderate size lesion in the caudal neostriatum. The lesion is shown at its maximal volume between stereotaxic levels L. 3.0 and L.4.0 according to the pigeon atlas (Karten & Hodos, 1967).



D-412

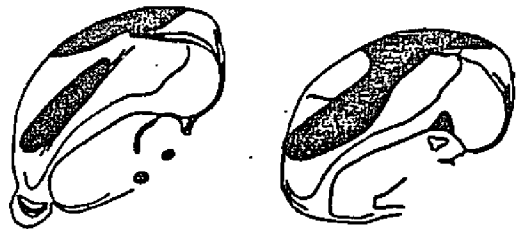


Fig. 18. Reconstruction of lesions through the visual wulst (HD and IHA), ventral hyperstriatum (HV), and ectostriatum (E). See sagittal key (Fig. 14) for locus of structural damage. Black areas indicate zones of necrosis. Section numbers indicate stereotaxic levels (Karten & Hodos, 1967) where lesions were made.



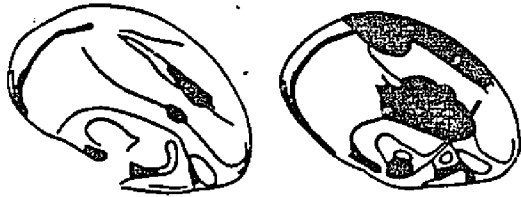
L1.0

L2.0



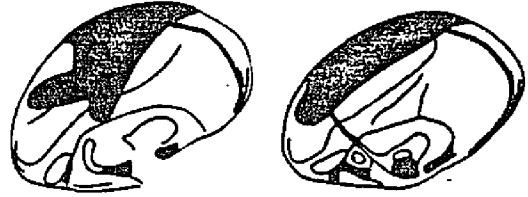
L1.0

L2.0



L3.0

L4.0



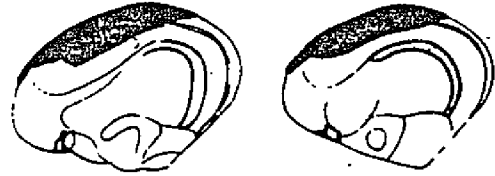
L3.0

L4.0



L5.0

L6.0



L5.0

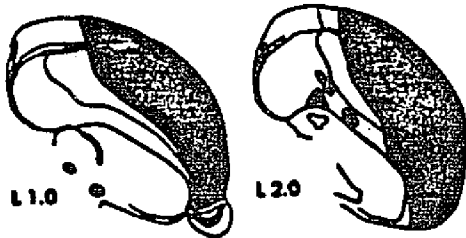
L6.0



L7.0



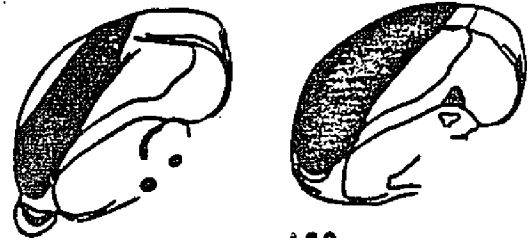
L7.0



L1.0

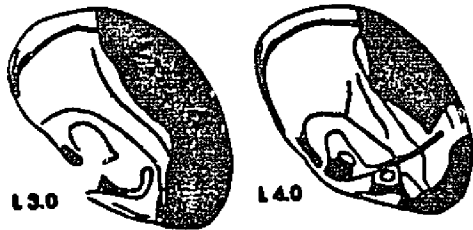
L2.0

D-409



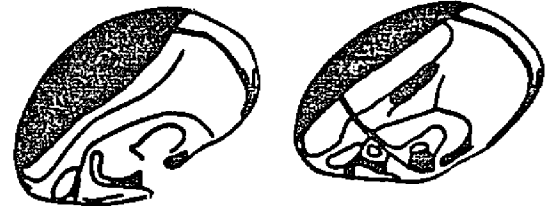
L1.0

L2.0



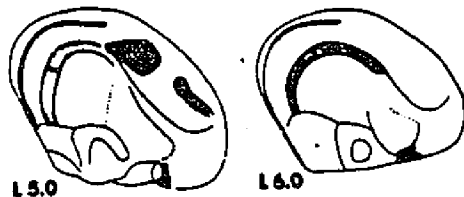
L3.0

L4.0



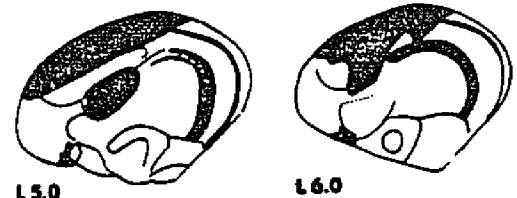
L3.0

L4.0



L5.0

L6.0



L5.0

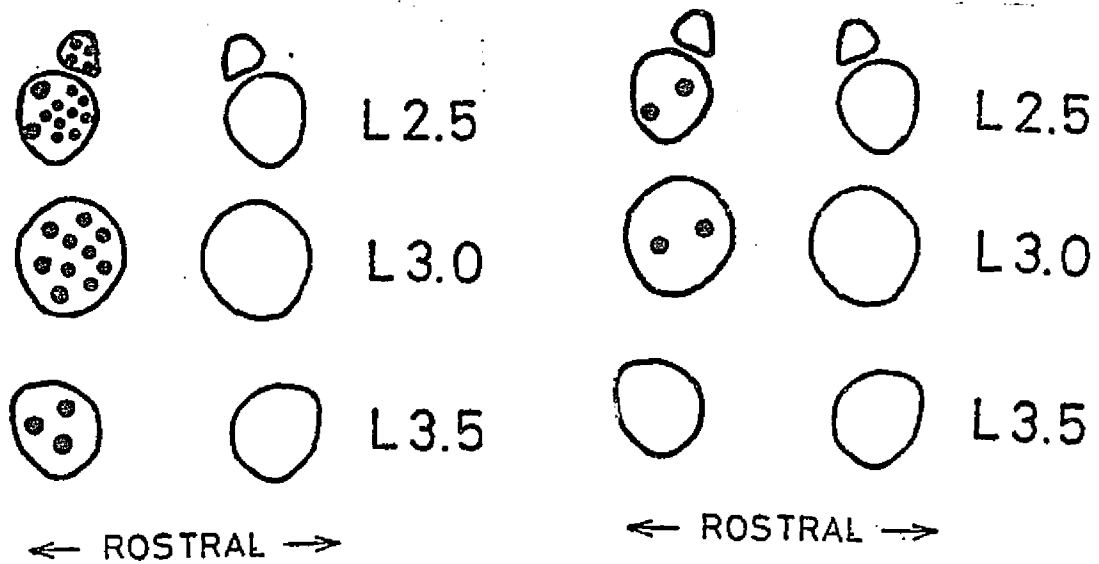
L6.0



L7.0



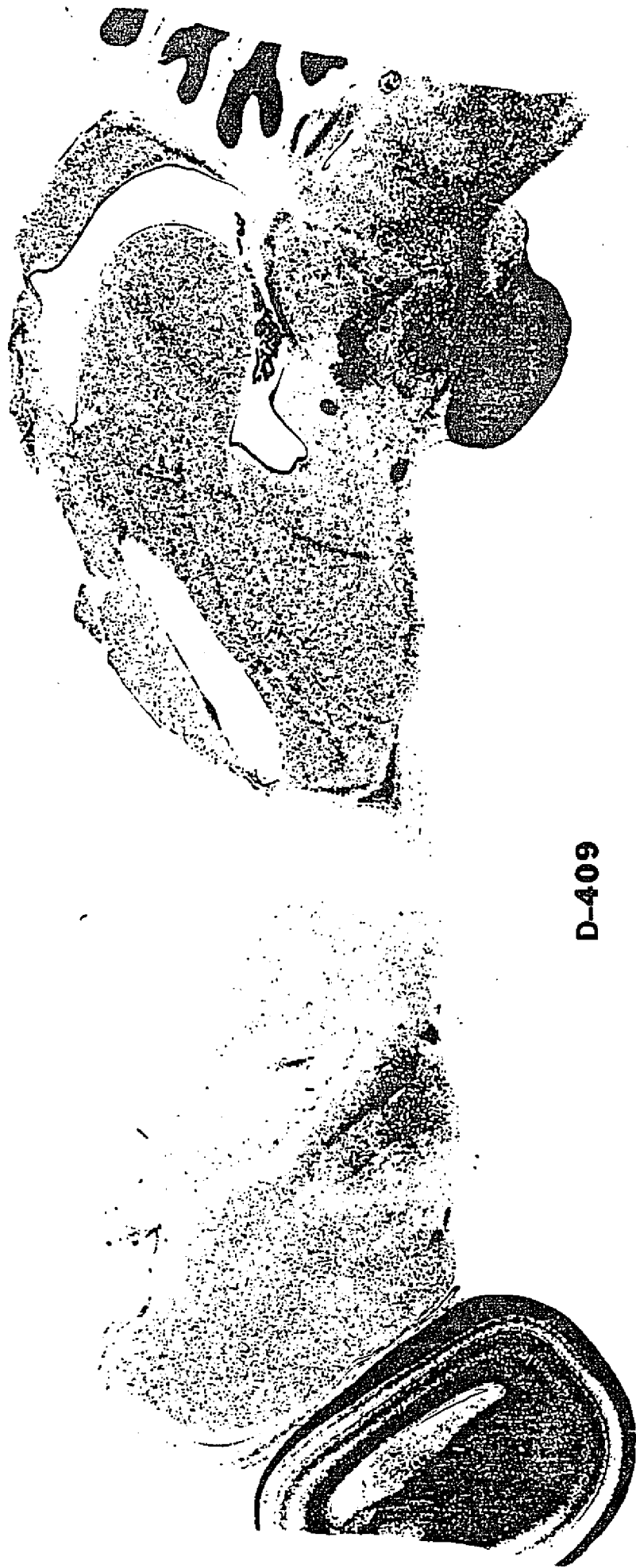
L7.0

**D-409****D-357**

- Occasional chromatolytic cells
- Considerable chromatolysis
with some cell loss
- Extensive cell loss, chromatolysis

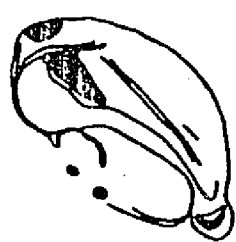
Fig. 19. A sagittal plane reconstruction of the extent of retrograde degeneration in nucleus rotundus following unilateral damage to the ectostriatum (E) and bilateral damage to the ventral hyperstriatum (HV) and the visual wulst (HD and IHA).

Fig. 20. A microphotograph illustrating one type of mixed lesion case. Between stereotaxic levels L. 1.0 and L. 4.0 damage to the visual wulst was complete. However, at more lateral levels (L. 4.0 - L. 6.0) the lesion invaded the ventral hyperstriatum (HV) and the ectostriatum (E). (Magnification 10X)



D-409

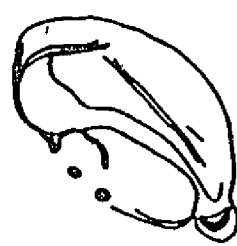
Fig. 21. Reconstructions of lesions through the ventral hyperstriatum (HV) that deafferented the visual wulst (HD and IHA). Black areas indicate zones of necrosis. Section numbers indicate stereotaxic levels (Karten & Hodos, 1967) at which lesions were made.



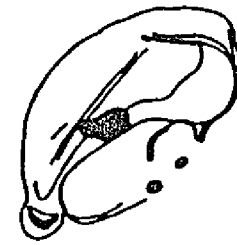
L1.0



L1.0



L1.0



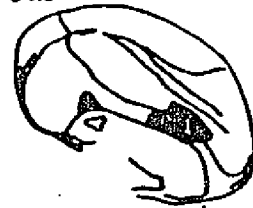
L1.0



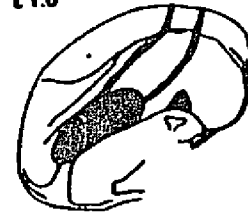
L2.0



L2.0



L2.0



L2.0



L3.0



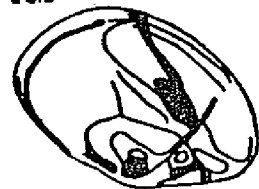
L3.0



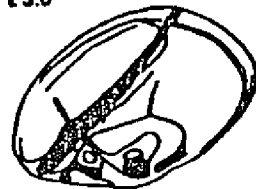
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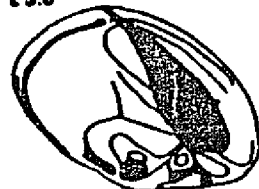
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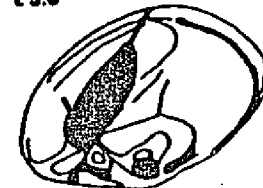
L4.0



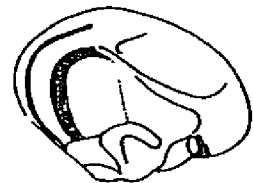
L4.0



L4.0



L4.0



L5.0



L5.0



L5.0



L5.0

D-538

D-405

neostriatum which border paleostriatum and nucleus basalis.

Case D-538 sustained a very slight bilateral lesion in the ventral hyperstriatum and a minimal infringement on the adjoining frontal and intermediate portions of the neostriatum (Fig. 21). However, the lesion succeeded in bilaterally transecting the fronto-thalamic tract thereby deafferenting the visual wulst laminae.

Postoperative Behavioral Results

Immediately after postoperative recovery, pigeons D-357 and D-409 showed signs of sensory defects by "misreaching" for food and water containers in the home cage. However, these symptoms quickly abated and disappeared entirely after two weeks. There were no postoperative indications of post-ural, motor, feeding, or sensory defects in any of the other birds.

Pattern Discrimination Retention

Table 3 lists the number of preoperative and postoperative discrimination training trials each bird required to reach a criterion of 90% correct in the 0% noise condition. The savings score each bird obtained is also indicated.

Normal Control Results

D-410, which served as an unoperated control, was allowed to rest for a period of 3 weeks after a stable noise

Table 3. PREOPERATIVE AND POSTOPERATIVE NUMBER OF DISCRIMINATION
TRAINING TRIALS REQUIRED TO REACH FIRST ASSESSMENT

Pigeon	Preoperative # Training Trials	Postoperative # Training Trials	Lesion	Percent Savings or Loss
			ECTOSTRIATUM	
D-355	1008	1427		-41
D-408	2016	1416		+30
D-273	1625	1008		+38
D-414	1008	0		+100
			VISUAL WULST	
D-358	672	1316		-96
D-520	2688	336		+88
D-537	1919	0		+100
			CAUDAL NEOSTRIATUM	
D-464	1586	0		+100
D-412	1032	0		+100
			MIXED LESIONS	
D-357	672	1680		-105
D-409	414	1008		-104
D-405	2688	336		+88
D-538	2185	0		+100
			NORMAL CONTROL	
D-410	1407	0		+100

interference index was obtained. Upon resumption of testing, D-414 displayed perfect retention of the no-noise pattern discrimination.

Ectostriatum Lesion Results

The total number of initial postoperative discrimination and intervening training trials resulting from this group's failure to reach criterion and maintain the discrimination amounted to 11,243 trials, 6,803 of which D-355 required. Pigeons D-273 and D-408 both sustained moderate damage of ectostriatum and failed to retain the discrimination. Thus, in the no-noise condition, pigeon D-355 with the largest and most complete destruction of ectostriatum exhibited the most severe impairment in relearning and maintaining the pattern discrimination, while pigeon D-414 with a minimal lesion of the ectostriatum demonstrated perfect retention and good maintenance of the pattern discrimination.

Visual Wulst Lesion Results

Pigeon D-537 with a lesion restricted to the visual wulst exhibited perfect retention in the no-noise discrimination.

Pigeon D-520 which sustained extensive damage to the visual wulst and minimal damage to adjoining areas of the ventral hyperstriatum required only 1 session of discrimination retraining, demonstrating a savings of 88%.

Pigeon D-358 which presented extensive damage to the visual wulst and slight damage to underlying areas of the ventral hyperstriatum required 4 sessions of discrimination retraining with no savings in retention.

Control Lesion Results

Both pigeons D-412 and D-464 with slight to moderate lesions of caudal neostriatum exhibited perfect retention in the no-noise discrimination.

Mixed Lesion Results

Pigeons D-357 and D-409 both displayed the largest size lesions (see Table 2). Both birds also underwent protracted discrimination retraining due to their inability to pass assessment (see Table 3) and maintain the no-noise discrimination once the assessment criterion was met. Thus, the number of postoperative discrimination training trials greatly exceeded the number given preoperatively. D-357 required almost 3 times as many postoperative trials to reach criterion and to pass assessment.

Pigeon D-405 which suffered a deafferentation of the visual wulst but only slight damage to the ventral hyperstriatum and visual wulst proper required only 1 session of discrimination retraining demonstrating a savings of 88%.

Pigeon D-538 which also suffered visual wulst deafferent-

tation via a slight lesion in ventral hyperstriatum demonstrated a perfect retention of the no-noise pattern discrimination.

Three cases (D-357, D-358 and D-409) which presented combinations of ectostriatum, visual wulst and ventral hyperstriatum lesions were equally deficient or more deficient in retention than those cases sustaining damage to ectostriatum proper. The lesion volume for the combined lesion cases was equal to or greater than that of the ectostriatum cases.

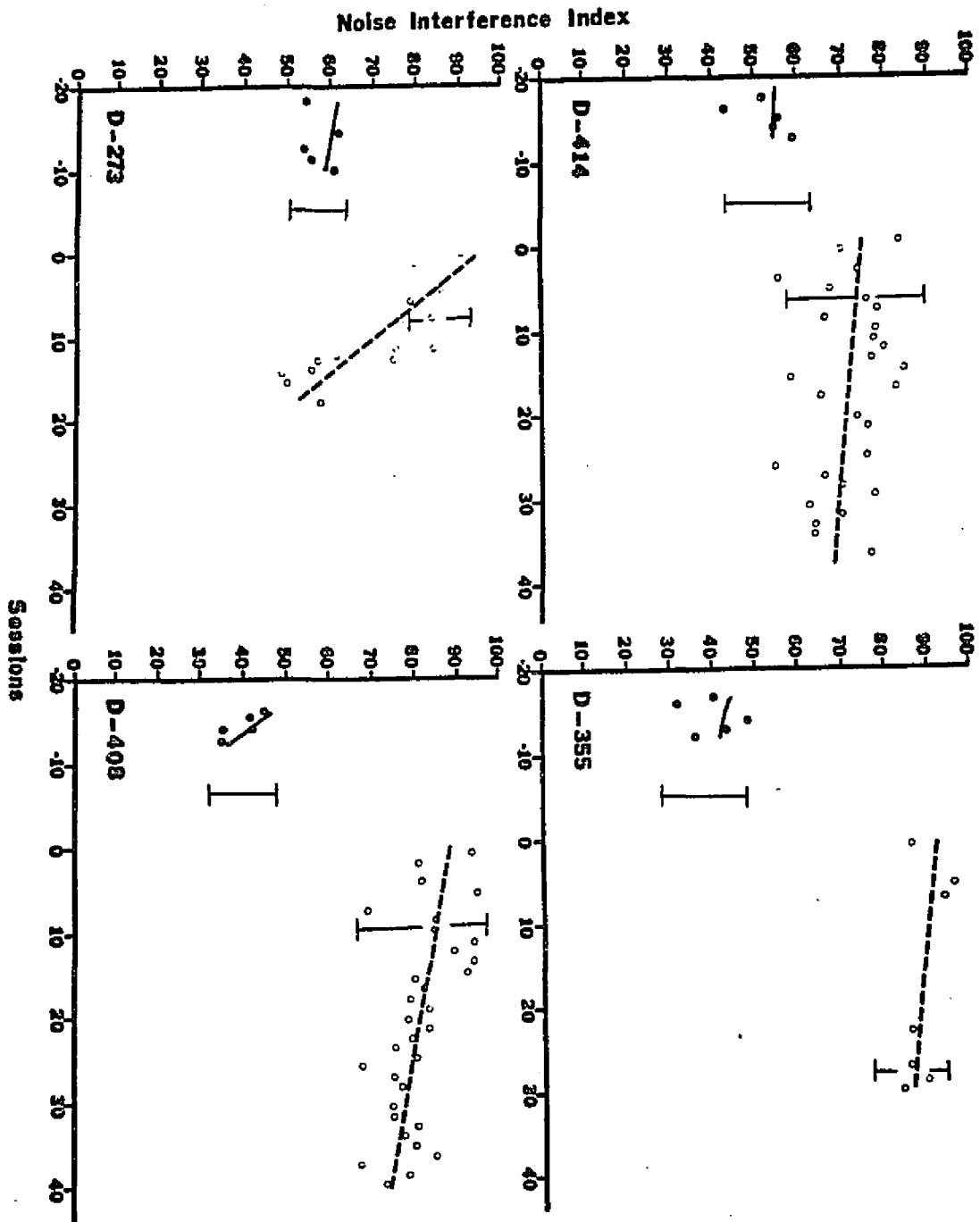
In order to determine whether the retention deficits were a function of lesion volume or lesion locus, a series of Pearson product-moment correlation coefficients (\underline{r}) were calculated between the (x) variables (total lesion volume, lesion volume at each locus) and the (y) variable (savings score in retention). The Pearson product-moment correlation coefficients for $n = 14$ between the savings scores of discrimination retention trials and the lesion loci were not significant ($\underline{r} = -.52, p < .10$ for ectostriatum damage; $\underline{r} = -.54, p < .10$ for ventral hyperstriate damage, $\underline{r} = -.37, p < .20$ for visual wulst damage). However, the correlation coefficient between the total lesion volume and savings scores was significant ($\underline{r} = -.64, p < .05$). The correlation coefficient between the percentage of ectostriatum damage and total lesion volume was minimal ($\underline{r} = -.07$). Whereas, the extent of damage to both the ventral hyperstriatum and the visual wulst was highly correla-

ted with total lesion volume ($\underline{r} = .94$, $p < .001$ for HV; $\underline{r} = .73$, $p < .01$ for visual wulst). Because there was a substantial covariance among total lesion volume, total damage to visual wulst, and total damage to ventral hyperstriatum, a partial correlation (Hayes, 1963) was calculated in order to determine the relative contribution of the specific locus of lesions to the deficits in retention. The coefficient of partial correlation $r_{xy.z}$ indicates the degree of statistical relation between the observed behavioral deficit (y) and the amount of destruction of one component of the visual system when the effects due to another component (z) are held constant. The partial correlation between the volume of damage in ectostriatum and the retention savings scores holding total lesion volume constant was significant ($\underline{r} = -.76$, $p < .001$). The partial correlation between ventral hyperstriatum damage and savings and that between visual wulst and savings scores were very low and not significant ($\underline{r} = .23$ for ventral hyperstriatum; $\underline{r} = .19$ for visual wulst).

Noise-Embedded Pattern Discrimination

The six curves that had been fitted to the preoperative noise interference index functions in Experiment I were also fitted to the postoperative index functions. Figures 22-25 present graphic comparisons of the best fitting postoperative functions with the last 5 preoperative sessions of stable per-

Fig. 22. Lines of best fit for the noise interference function for each pigeon sustaining bilateral lesions of the ectostriatum. Scatter diagrams of the actual data points of each bird are superimposed on the line of best fit for thatbird. Only the last five preoperative sessions are shown. The bars placed between the pre- and postoperative functions represent the confidence interval obtained for the mean preoperative stability performance. The bars superimposed on the postoperative function represent the confidence interval obtained during the first five days of postoperative testing.



formance. The noise interference index is plotted as a function of successive sessions.

Pearson-Product moment correlations were again used to evaluate the goodness of fit between the observed values and the expected frequencies predicted by the least-squares fit (see Table 4). The bars placed between the pre- and post-operative functions represent the confidence intervals obtained for the mean interference index obtained during the first five days of postoperative testing.

A Student's t-Test for repeated measures (Winer, 1962) was used to assess the significance of the differences obtained between the means of the stable preoperative indexes and the initial 5 postoperative indexes (see Table 5).

Normal Control Results

D-410, the unoperated control, met its preoperative range of stable indexes within 5 sessions after a rest period of 3 weeks.

Ectostriatum Lesion Results

The total number of postoperative test sessions ranged from 21 to 39 with a mean of 31.8. Except for pigeon D-273 who was able to meet its preoperative stability criterion, the remaining 3 birds were tested at least until they had performed the minimum number of sessions given to meet pre-

Table 4. PREOPERATIVE AND POSTOPERATIVE CURVES OF BEST FIT FOR
NOISE INTERFERENCE FUNCTIONS

Pigeon	Preoperative Curve of Best Fit	r	Lesion	Postoperative Curve of Best Fit	r
D-355	$Y = 23.73 + 484.27/X$.87	ECTO- STRIATUM	$Y = 92.28 - .21X$.43
D-408	$Y = 129.51 - 2.37X$.90		$Y = 88.92 - .41X$.46
D-273	$Y = 39.62 + 1199.03/X$.87		$Y = 108.68 - 2.32X$.82
D-414	$Y = 52.61 + 119.08/X$.47		$Y = 76.61 - .27X$.24
D-357	$Y = 1/ (.002 + .002X)$.95	MIXED LESIONS	$Y = X/ (-.031 + .015X)$.18
D-409	$Y = 108.60 (-.04x)$.78		$Y = 92.40 - 1.67X$.81
D-538	$Y = 127.84 - 2.79X$.93		$Y = 1/ (.015 + .001X)$.55
D-405	$Y = -2.56 + 902.38/X$.90		$Y = 1/ (.007 + .001X)$.81
D-520	$Y = 23.40 + 1086.37/X$.87	VISUAL WULST	$Y = 14.90 + 596/X$.76
D-358	$Y = 23.55 + 1086.33/X$.85		$Y = 14.85 + 595.97/X$.74
D-537	$Y = 35.89 + 422.63/X$.69		$Y = 54.42 - 7.12/X$.66
D-464	$Y = 40.92 + 298.51/X$.84	CAUDAL NEO- STRIATUM	$Y = 53.60 + 6.30/X$.47
D-412	$Y = 107.92 - 2.01X$.91		$Y = 44.62 - .58X$.21
D-410	$Y = 32.28 + 546.05/X$.77	NORMAL CONTROL	$Y = 47.74 + 15.43/X$.52

Table 5. PREOPERATIVE AND POSTOPERATIVE COMPARISON OF NOISE INTERFERENCE INDEX VALUES

Pigeon	Preoperative		Postoperative		Initial	Postoperative		Final
	Final		Initial		Difference	Final		Difference
ECTOSTRIATUM								
D-355	39.39	8.06	88.04	5.90	48.65	86.60	4.47	47.21
D-408	38.50	4.46	81.63	13.55	43.13	76.13	8.89	37.63
D-273	57.33	5.18	86.51	5.58	29.18	54.74	5.66	-2.59
D-414	54.50	7.89	71.88	13.79	17.38	66.41	7.93	11.91
					t = 9.71**			
						t = 2.05 (NS)		
VISUAL WULST								
D-358	43.33	3.76	61.29	16.88	17.96	42.95	7.87	-.38
D-537	53.84	2.40	51.17	3.46	-2.67	51.17	3.47	-2.67
D-520	39.92	5.02	57.20	3.71	17.28	39.80	3.31	-.12
					t = 1.60 (NS)			
						t = 1.31 (NS)		
MIXED LESIONS								
D-409	38.20	5.50	86.10	12.12	47.90	42.75	12.25	4.55
D-357	36.79	3.20	73.29	9.40	36.51	80.35	11.54	43.56
D-538	47.25	7.36	57.75	6.22	10.50	54.50	8.56	7.25
D-405	43.15	6.00	58.94	8.90	15.79	39.39	5.71	-3.76
					t = 3.156*			
						t = 1.23 (NS)		
CAUDAL NEOSTRIATUM								
D-464	51.04	5.89	55.41	4.17	4.37	55.08	3.56	4.04
D-412	52.79	5.79	41.84	7.89	-10.95	39.38	3.64	-13.41
					t = .67 (NS)			
						t = .54 (NS)		

** Significant at .01 level of confidence

* Significant at .05 level of confidence

(NS) Not Significant

operative index stability.

The total number of postoperative psychophysical test trials ranged from 3,456 to 9,504. Both D-408 and D-414 performed more psychophysical trials postoperatively than preoperatively (1,728 and 2,016 respectively). Although D-355 was given more postoperative than preoperative sessions, D-355 performed fewer psychophysical test trials because of numerous intervening training trials resulting from its failure to pass assessment. However, D-355 was not tested beyond 34 sessions since the psychophysical test performance given in session 9 by D-355 was almost the same as that rendered in session 34. D-273 required considerably less postoperative psychophysical trials to meet preoperative stability levels. Thus, those pigeons with either large or small bilateral lesions, as verified by extensive or slight bilateral rotundal degeneration, failed to meet their preoperative stability criterion. Whereas, D-273 with moderate but essentially unilateral lesion, as evidenced by extensive rotundal degeneration on one side and slight degeneration on the other, was able to meet its preoperative criterion with a savings of 50%. As shown in Figure 22, there is no overlap in the final preoperative and the initial postoperative confidence intervals except in case D-414 which displayed a minimal lesion in ectostriatum. The final postoperative indexes obtained for the other 3 birds were considerably higher than those obtained preoperatively.

For example, Figure 22 shows that D-355 stabilized preoperatively at a mean interference index of 39.0 but after suffering an almost complete bilateral ectostriate lesion, D-355 exhibited a severe deficit, and finished postoperative testing with a comparatively high interference index ($\bar{X} = 86.6$). The lowest index obtained was 81.9. Thus, D-355 could not perform the discrimination with more than 7-18% noise in the background despite extended retraining. The differences in discrimination performance found between the last 5 preoperative days and the first 5 postoperative days proved significant at the .01 level of confidence. Moreover, with the exception of D-273, the remaining postoperative performance was confined within the confidence intervals obtained for the first 5 sessions of postoperative performance. Thus, unlike the results of Experiment I, practice does not appear to facilitate visual noise tolerance in those cases which have moderate to extensive lesions in ectostriatum. More importantly, extensive damage of the ectostriatum appears to substantially reduce the visual channel capacity for pattern-noise input. This finding is made obvious by the flat functions obtained for birds sustaining moderate to extensive damage of ectostriatum.

Visual Wulst Lesion Results

Pigeons D-358 and D-520 both sustained extensive injury of visual wulst and slight damage of ventral hyperstriatum

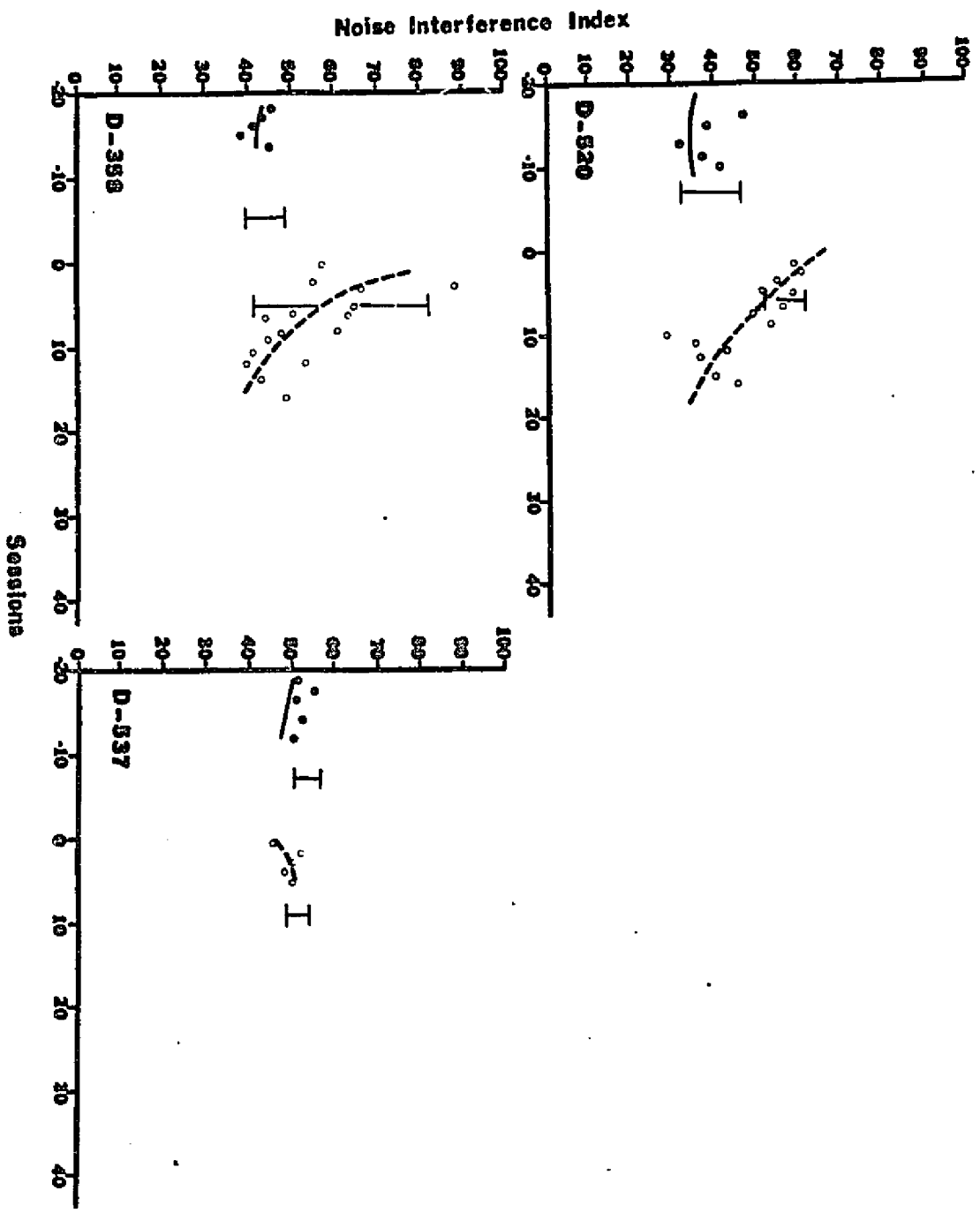
and both demonstrated a similar performance of the noise-embedded pattern discrimination (see Fig. 23). That is, both D-358 and D-520 required postoperative practice to reach preoperative efficiency in discriminating the noise-embedded patterns; but both were able to regain their preoperative noise interference indexes with nearly the same amount of practice (16 sessions for D-358 and 15 sessions for D-520).

Pigeon D-537 with a moderate to extensive lesion of the visual wulst exhibited perfect retention of the noise-embedded discrimination. That is, D-537 met its stable preoperative index values within 5 postoperative sessions (Fig. 23). Overall, the pre- and postoperative index differences were considerably smaller than those obtained by the ectostriatum group and were not found to be significant in a t-Test (see Table 5). Moreover, birds suffering extensive visual wulst damage are able to improve their tolerance for visual noise with practice and quickly reach their preoperative channel capacity for pattern-noise input (compare Figs. 8 & 23).

Mixed Lesion Results

Pigeon D-357 sustained extensive damage to the visual wulst and adjoining areas and was not able to stabilize its postoperative performance or regain its preoperative interference index within the required number of preoperative

Fig. 23. Curves of best fit for the noise interference function for each pigeon sustaining bilateral lesions of the visual wulst. Scatter diagrams of the actual data points of each bird are superimposed on the curve of best fit for that bird. Only the last five preoperative sessions are shown. The bars placed between the pre- and postoperative functions represent the confidence interval obtained for the mean interference index obtained during preoperative stability performance. The bars superimposed on the postoperative function represent the confidence interval obtained for the mean interference index obtained during the first five days of postoperative testing.



sessions. However, D-357's overall postoperative discrimination performance was considerably better than that of birds suffering extensive or moderate injury of ectostriatum.

Pigeon D-409 also sustained damage which extended from visual wulst to ectostriatum. D-409 also was not able to regain its preoperative index level. But like D-357, D-409 performed better than pigeons in the ectostriate group since it was able to improve its index with protracted retraining.

Pigeon D-405, with a minimal invasion of the ventral hyperstriatum that undercut the visual wulst, was able to regain its preoperative index level in considerably fewer postoperative trials.

Pigeon D-358 had a similar type lesion and was able to reach its range of stable preoperative indexes within the first 5 postoperative sessions.

For all the mixed lesion cases, the differences between the noise indexes obtained for the last 5 preoperative sessions and the first 5 postoperative sessions were significant at the .05 level of confidence. However, the difference between the final preoperative and postoperative indexes were not significant (see Table 5 and Fig. 24).

Control Lesion Results

Both pigeons D-412 and D-464 with slight to moderate lesions of caudal neostriatum also met preoperative stability

Fig. 24. Curves of best fit for noise interference function for each pigeon in the mixed-lesion group. Scatter diagrams of the actual data points of each bird are superimposed on the line of best fit for that bird. Only the last five preoperative sessions are shown. The bars placed between the pre- and postoperative functions represent the confidence interval obtained for the mean preoperative stability performance. The bars superimposed on the postoperative function represent the confidence interval obtained during the first five days of postoperative testing.

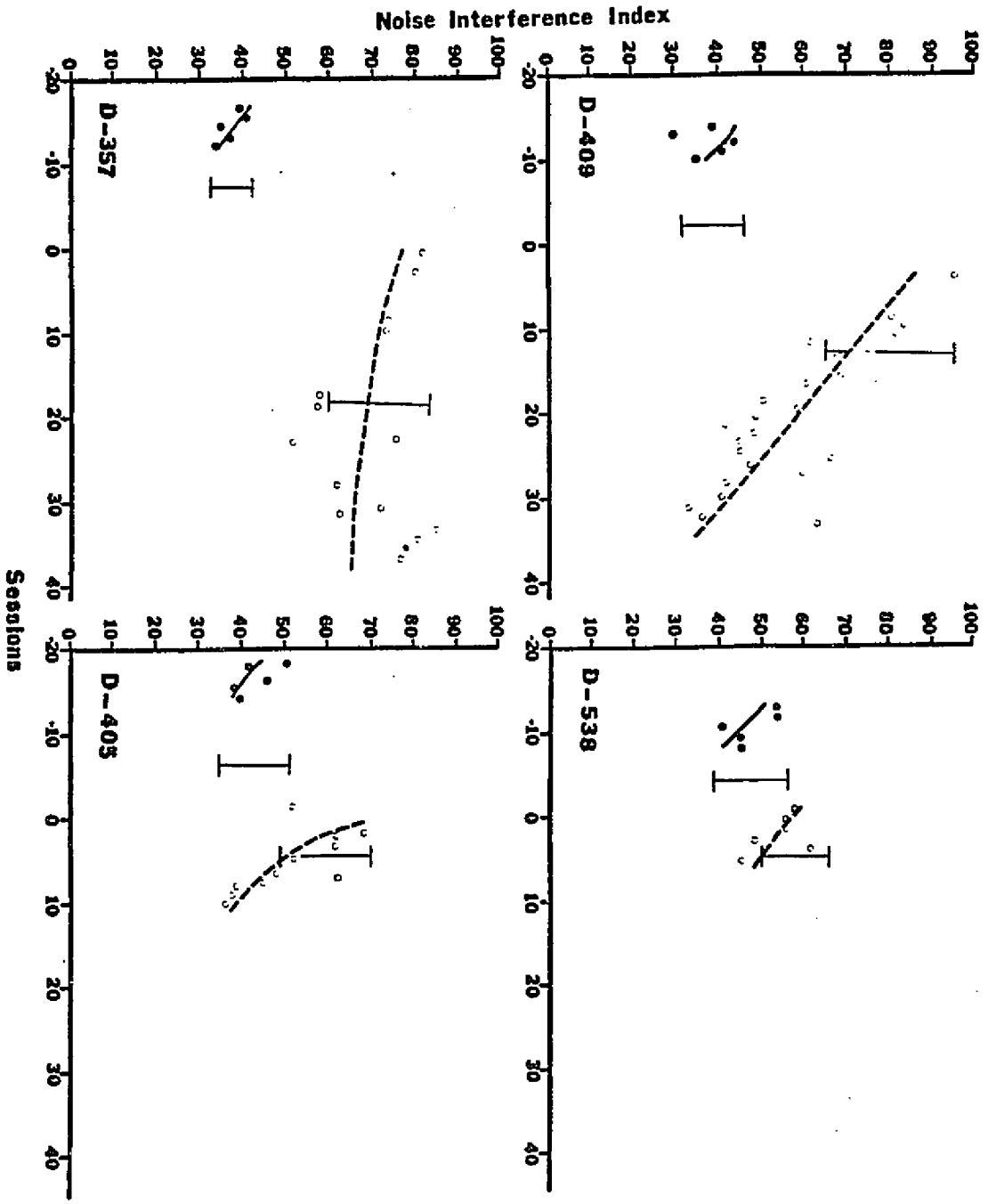
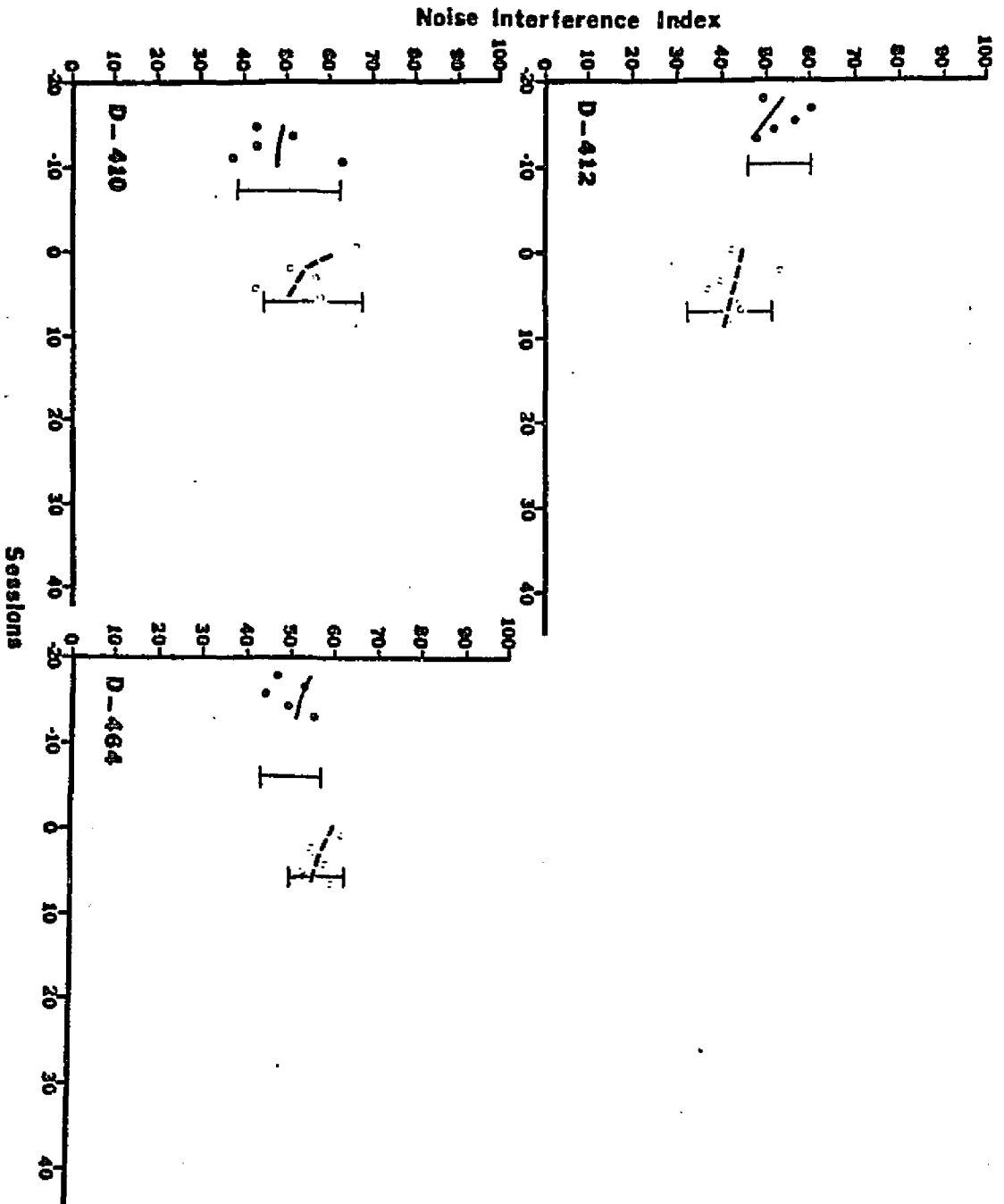


Fig. 25. Curves of best fit for the noise interference function for each pigeon in the control group. Scatter diagrams of the actual data points of each bird are superimposed on the line of best fit for that bird. Only the last five preoperative sessions are shown. The bars placed between the pre- and postoperative functions represent the confidence interval obtained for the mean preoperative stability performance. The bars superimposed on the postoperative function represent the confidence interval obtained for the mean interference index obtained during the first five days of postoperative testing or retention testing.



ranges within the first 5 postoperative sessions (Fig. 25). t-tests of course showed no significant differences between pre- and postoperative stability means (see Table 5).

Summary of Results

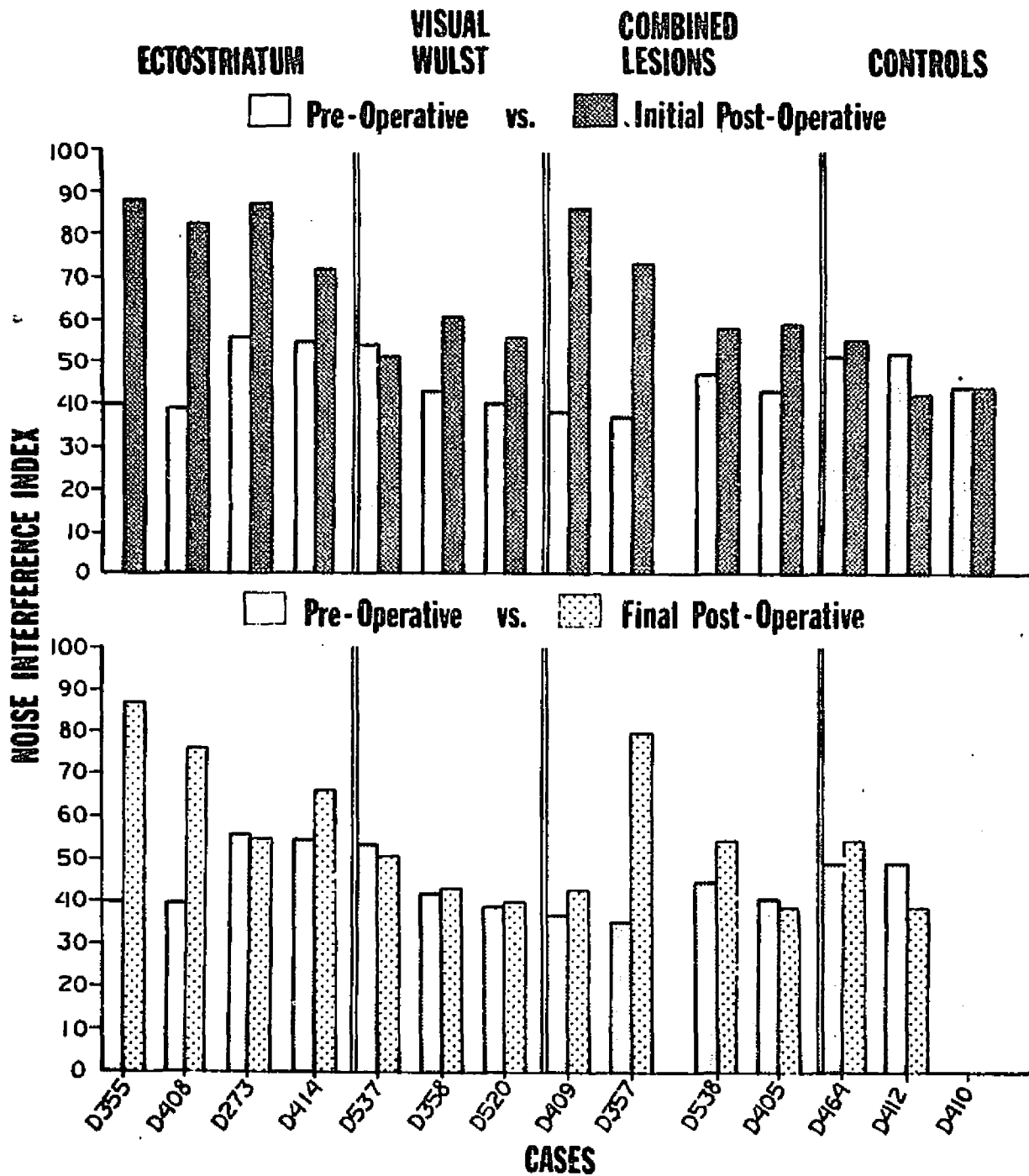
Figure 26 presents a summary of the initial and final differences that were observed in the noise interference index after telencephalic lesions. All birds with ectostriatal damage displayed considerable losses in noise tolerance during the initial postoperative sessions. Permanent deficits in the noise interference index were apparent in those 3 birds which manifested bilateral and symmetrical degeneration of rotundus (D-355, D-408, D-414).

Those cases having a combination of ectostriate, visual wulst and ventral hyperstriate lesions (D-357, D-409) also showed considerable losses initially. However, D-409 reached its preoperative range of noise tolerance by the end of postoperative testing; whereas, D-357 showed a permanent deficit at the end of postoperative testing.

Those cases which suffered deafferentation of the visual wulst (D-405 and D-538) via damage to HV gave a similar postoperative performance. Both showed initial deficits but no permanent deficits.

Two out of three birds sustaining visual wulst injury did show initial deficits but did not show any permanent impairment.

Fig. 26. A summary of pre- and postoperative behavioral results for all groups. In the upper graph the mean of the stable preoperative interference index is compared with the interference index obtained during the first five postoperative sessions. In the lower graph the mean preoperative index is compared with the index obtained during the final five days of postoperative testing.



The operated controls, i.e., the 2 pigeons with caudal neostriatal injury, performed like the normal control (D-410), i.e., they did not show any initial or permanent deficit.

As can be seen in Figure 26, the largest initial and permanent deficits were displayed by those pigeons that suffered damage to the ectostriatum.

DISCUSSION

Experiment II has shown that pigeons with moderate to large ectostriate lesions (D-355, D-408, D-273) cannot retain a visual discrimination of patterns presented successively but are only able to relearn the discrimination with protracted retraining (see Table 3). This result is consistent with those reports of previous effects of ectostriate lesions on pattern discrimination (Hodos & Karten, 1970). The same result is true of pigeons that exhibited combinations of ectostriatum, visual wulst and ventral hyperstriatum lesions (D-357, D-409). Conversely, two out of three pigeons with moderate to extensive injury of visual wulst (D-537, D-520) performed as well as the unoperated pigeon (D-410), i.e., they exhibited perfect retention. The pigeons with slight damage of only caudal neostriatum or ventral hyperstriatum also exhibited perfect retention. Thus, the foregoing results support the long standing conclusion that lesions of ectostriatum produce a severe impairment on coarse measures of pattern discrimination, while extensive damage of the visual wulst or caudal neostriatum yields little or no performance deficit on coarse measures of pattern discrimination. Yet, when an extensive lesion of the visual wulst is combined with a minimal lesion of the ectostriatum (D-357), a performance deficit that is equal to or greater in magnitude results than would occur with ectostriatal injury

alone. This finding also confirms those found in earlier studies of the effects of combined tectofugal and thalamofugal pathway lesions on coarse intensity and pattern discriminations (Hodos, Karten & Bonbright, 1973; Jarvis, 1974). Even so, all pigeons in the present study were able to reacquire the coarse pattern discrimination regardless of the lesion locus. This finding was also expected since it had been decided earlier that the coarse discrimination method of assessing visual impairments was too insensitive to subtle visual defects to reveal permanent deficits (Hodos & Bonbright, 1974). Therefore, in the present study, a more challenging test of visual pattern processing was devised in which the channel capacity of the pigeon visual system for pattern discrimination was measured. A pattern recognition paradigm was employed in which the pigeons were systematically forced to recognize and distinguish the same patterns used in the coarse discrimination when they were embedded in increasing percentages of background noise. The pattern recognition paradigm was employed rather than a discrimination learning paradigm in order to achieve a controlled situation in which the pigeons' behavior was not a function of discrimination learning, i.e., familiarity with pattern complexes, but of the discriminial difficulty of the pattern complex.

Table 5 shows the initial and final differences that were observed in the visual channel capacity for pattern and noise

as indicated by the noise interference index. Postoperatively, all birds with lesions of ectostriatum displayed losses in noise tolerance during the initial postoperative sessions. Moreover, permanent deficits in the noise interference index were apparent in those birds having ectostriatal lesions which transected the thalamofrontal tract and induced secondary degeneration of rotundus in the thalamus (D-355, D-408, D-414). As shown in Figure 22, the best fitting functions for all subjects with damage of ectostriatum were linear. This was not true of the preoperative functions, where 3 out of 4 were hyperbolic. This change in response is noteworthy in view of the assumptions of signal detection and neural quantum theory (Barlow, 1961; Green & Swets, 1966). Thus, one may be tempted to speculate that these linear functions are responses to an overwhelming addition of internal noise imposed on the bird's visual system by ectostriatal lesions. The slopes of these linear functions in 3 out of 4 cases did not differ significantly from 0 even though the postoperative test sessions were numerous. Thus, increasing the practice had no effect upon the efficiency of noise-embedded pattern discrimination, suggesting that severe ectostriatal lesions limit the amount of pattern information that can be transmitted or that pigeons with severe disruption of the tectofugal pathways are unable to habituate to visual noise or suppress the effects of visual noise stimulation. The fact that practice has very

little effect in decreasing the noise interference index . . . firmly establishes that ectostriatal lesions adversely affect the accuracy of visual pattern processing and that the amount of this effect is a function of the amount of noise (external and internal) that is present.

However, visual wulst injury seems to have no effect on the discrimination of noise-embedded patterns. In spite of the greater discriminial difficulty imposed by the noise backgrounds, the pigeons having moderate to extensive visual wulst damage showed little if any initial impairment and no permanent deficits. Their lesions were as large as those of severely impaired pigeons in the ectostriate group. Moreover, the best fitting functions were hyperbolic for those pigeons with visual wulst damage. Therefore, the noise interference index decreased sharply and quickly reached the preoperative level. This quick recovery to preoperative levels of performance suggests that pigeons with visual wulst damage are able to behave like naive, intact pigeons, i.e., they are able (with practice) to habituate or suppress the effects of visual noise stimulation until the normal channel capacity for visual noise tolerance is reached. Thus, it would appear that increasing the discriminial difficulty of a learned pattern discrimination by embedding it in increasing amounts of background noise yields a test which specifically reveals visual defects resulting from tectofugal disruption.

Those pigeons which sustained a combination of ectostriate, visual wulst and ventral hyperstriate lesions (D-357, D-409) also showed considerable losses initially. However, D-409 reached its preoperative range of noise tolerance by the end of postoperative testing; whereas, D-357 showed a permanent deficit at the end of postoperative testing. Since the evidence in this study and in a previous study (Hodos, Karten & Bonbright, 1973) has established that extensive lesions in the thalamofugal pathway yield little or no deficits in coarse pattern discrimination tasks; the behavioral differences exhibited by D-409 and D-357 are most likely due to differences in ventral hyperstriate involvement since both birds suffered only minimal ectostriate damage with D-357 showing less damage to ectostriatum than D-409.

Ongoing studies of the effects of visual wulst lesions on visual acuity (Hodos, et al., in prep) provide corroborative evidence. Hodos (personal communication) explains that deficits in visual acuity are only apparent when wulst damage includes ventral hyperstriatum as well as IHA and HD. No acuity losses are evident when damage is restricted to IHA and HD portions. In addition, Pritz, Mead and Northcutt (1970) reported that visual wulst lesions which encroached on ventral hyperstriatum rendered initial deficits in pattern and intensity discrimination. While Tuge and Shima (1959) reported that complete ablation of the dorsal corticoid areas in combin-

ation with an almost complete destruction of the hyperstriatal complex prohibits discrimination of red and white light. Further evidence has been reported by Zeigler (1963) who demonstrated that lesions of the hyperstriatum which include both visual wulst and ventral hyperstriatum areas produce significant deficits in both learning and retention of pattern and brightness discrimination.

Ongoing anatomical studies also implicate the ventral hyperstriatum in visual function. Hodos and West (in prep) have demonstrated by means of autoradiography, a fiber projection from the periectostriatal belt to the ventral hyperstriatum. Ritchie (1979) injected horseradish peroxidase into the hyperstriatum ventrale and found labeled cells in the periectostriatal belt, and in the neostriatum which caps the rostral pole of ectostriatum.

Some results of the present study offer support for the hypothesis that ventral hyperstriate damage induces impairments in discrimination of embedded stimuli (see Table 2). The more damage a pigeon suffered in the ventral hyperstriatum, the more severe its deficit in discriminating patterns embedded in visual noise. Thus, the slight damage to hyperstriatum ventrale apparent in pigeons D-358, D-405 and D-520, which also manifested lesions in other telencephalic areas as large or larger than those of severely impaired pigeons in the ectostriate group did not induce any permanent deficits

in visual noise tolerance during pattern discrimination.

But rather, a deficit in visual noise tolerance is determined by a specific injury of ectostriatum or perhaps ventral hyperstriatum.

GENERAL DISCUSSION

Experiment I clearly demonstrated a basic limitation of the intact avian visual system: It can process noise-embedded figures until the system is overloaded by external noise. That is, the visual channel capacity for accurately processing pattern information was found to be limited by the amount of simultaneous background noise that could be processed. Thus, correct pattern discrimination was not much better than chance when the patterns were embedded in more than 50%-75% noise.

Experiment II demonstrated that the integrity of the tectofugal pathway is necessary for pigeons to visually discriminate two-dimensional patterns that are embedded in moderate amounts of static noise. This conclusion is justified since pigeons with lesions of the thalamofugal pathway demonstrate perfect retention when discriminating patterns against a noisy surround; whereas, birds suffering tectofugal pathway interruption as a result of injury to ectostriatum exhibit permanent deficits; i.e., they never approach preoperative performance levels and even minimal percentages of visual noise produce a marked deterioration of visual discrimination performance.

These results do not match those found in primate studies in which both lateral striate and temporal lesions result in impairment in the discrimination of embedded stimuli (Butter,

1969; 1972). As to possible interpretations of class differences in the effects of visual system lesions on discrimination of embedded figures, the quantitative difference in discrimination impairments obtained between pigeons with visual wulst and ectostriate lesions may be due to differences in methodology. The embedded-figures test employed in the present experiment systematically forced each subject to perform at the limits of its ability to extract information from a noisy stimulus channel. Thus, both the upper and lower limits of noise tolerance were determined for each subject. In the previously mentioned studies of embedded pattern discrimination (e.g., Butter, 1969; 1972; Atencio, et al., 1975), the irrelevant stimuli were not quantified and the degree of their interference was not systematically measured. Consequently, those subjects sustaining lateral striate lesions may have suffered only slight decreases in noise tolerance that were measured as severe deficits because the embedded tests used probably required the full capacity of noise tolerance for efficient pattern discrimination.

Another explanation for the class differences observed in embedded-pattern discrimination may lay in differences in the anatomical arrangement of the visual system. Fewer interconnections between tectofugal and thalamofugal pathways have been described at telencephalic levels in the pigeon. As a consequence, damage to one set of pathways may not signifi-

cantly affect the performance of the other. Whereas, the lateral striate lesions that were generally investigated in the primate studies (Butter, 1969; 1972) infringed on the foveal prestriate cortex, an area which sends fibers to inferotemporal cortex and receives fibers from striate cortex. Moreover, injury of the foveal prestriate cortex has produced a more severe impairment of visual pattern discrimination learning and retention than has injury of inferotemporal cortex (Iwai & Mishkin, 1968; Cowey & Gross, 1970). Thus, it is possible that the deficits in test performance shown by monkeys with lateral striate injury were due to the invasion of the ventral prestriate area.

The present experiment offers evidence against the suggestion that tectofugal impairments may be responsible for memory deficits. The perfect retention of an intact pigeon after 3 weeks of rest attests to the nonimpairment of memory mechanisms. Moreover, if pigeons with tectofugal lesions suffered a loss of visual memory, it would be difficult to explain their retention in discriminating the relevant stimuli under the no-noise conditions and in minimal noise surrounds. Likewise, the adverse effects of tectofugal lesions on noise-embedded discrimination were not confounded with a failure in S-R association since the pigeons subjected to ectostriate lesions were able to follow the proper stimulus-response sequences when the patterns were embedded in minimal percentages

of noise. Thus, the foregoing observations strongly suggest that the tectofugal pathway in pigeons does not appear to mediate visual memory or visual association but rather appears to be involved in the suppression of irrelevant aspects of the visual world.

Exactly how the tectofugal system mediates the suppression of irrelevant background stimulation is unknown. However, several electrophysiologists have suggested that the wide receptive fields, characteristic of tectofugal areas in primates and pigeons, are suited to mechanisms of selective attention (see Gross, et al., 1969; Salzen & Parker, 1974). Stimulus orientation and localization functions have been ascribed to these units since the receptive fields are large and maximally respond to movement (see Gross, 1973; Donovan, 1978, for review). However, the receptive field traits listed above do not suggest why pigeons with tectofugal lesions that are able to discriminate "static" visual patterns cannot continue to distinguish those same patterns when they are embedded in "static" visual noise.

Selective attention theories based on concepts of signal detection suggest that neural filter mechanisms determine the efficiency of embedded pattern discrimination. Broadbent (1958) first suggested that a "selective filter" in the brain rejects irrelevant or distracting stimulation before its content is fully analyzed. Treisman (1964) maintained that

neural noise results when central nervous system transmission pathways are altered and that the resulting noise interferes with discriminative capacities. Likewise, Hodos and Bonbright (1974) maintain that once the telencephalic filter mechanisms have been obstructed or incapacitated via degeneration or ablation, the irrelevant stimulation will enter the same information channel as the relevant stimulus, adding to the noise already present in that channel. The resultant increase in noise would decrease the perception of the relevant stimulus. Some results of the present study support these contentions since after tectofugal damage, the pigeon's success in performing the embedded-pattern discrimination dropped drastically when more than 12-25% noise was added to the background. Thus, it would seem that damage to the tectofugal tract increases the internal noise which in turn induces discrimination deficits to the same degree that high percentages of external noise (75%) impair discrimination in intact pigeons. If this is the case, then the ectostriatum may operate as an optimal filter which improves the pattern-to-noise ratio by suppressing the interfering effects of background noise. This was not the case when the visual wulst was damaged. Contrary to the predictions of Hodos and Bonbright (1974), the visual channel capacity did not change in pigeons with lesions restricted to the visual wulst. Thus, the visual wulst does not seem to operate as an optimal filter to improve the signal-

to-noise ratio during visual transmission.

The actual neural mechanism which the tectofugal system implements to suppress visual noise was not suggested by the filter theories. But as mentioned earlier, a likely candidate would be a lateral interactive mechanism. The anatomical arrangement of the pigeon retina is conducive to a high frequency of lateral interaction during visual processing (see Donovan, 1978). Thus, the injury of the wide-field ectostriatal cells could have altered the inhibitory mechanisms such that contours between the target stimuli and noise backgrounds could no longer be enhanced.

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